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THE FOSSIL HORSES OF THE TEXAS GULF COASTAL PLAIN: A REVISION

by

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THE FOSSIL HORSES OF THE TEXAS GULF COASTAL PLAIN: A REVISION

By Ann Forsten[1]

ABSTRACT

Sixteen species of nine genera of fossil horses from the Texas Gulf Coastal Plain are redescribed or described and compared with forms known from other areas of North America. Similar forms are found to occur especially in faunas of the Great Plains, Florida, and the West Coast. The evolution of the coastal plain horses and their presumed phylogenetic importance is discussed. The fossil horses are shown generally to confirm Patton's (1969) correlation of the four local faunas of the Texas Gulf Coastal Plain.

INTRODUCTION

The faunas of the Texas Gulf Coastal Plain have been described in a series of publications. Wilson (1957, 1960) published on the entelodonts and carnivores, and Patton (1969) on the artiodactyls. In 1955 Quinn gave a detailed description of some of the Equidae, earlier described in part by Hay (1924) and reported on by Hesse (1942) and Quinn (1952).

The material I worked on is the same as Quinn (1955) studied, with some later additions, but includes the anchitheriines and hipparions which Quinn omitted or only briefly mentioned. Dr. S. David Webb is presently studying the sample of *Pseudhipparion* from the Lapara Creek fauna, and will report on that genus later. The aim of this revision is to clarify the taxonomy of the fossil horses of the Texas Gulf Coastal Plain, and to compare them with contemporaneous forms from the Great Plains, the Great Basin, and the Pacific Coast. These problems have remained largely unsolved, due to extreme horizontal splitting of the taxa. To facilitate comparisons, a redescription of the samples of the species I consider valid seemed necessary, since Quinn (1955) did not stress the variation in visual morphology in each species, nor was this variation apparent in his descriptions, because of the low number of referred specimens in each taxon. I also consider a description of the referred limb bone material necessary, since the skeleton may reveal as significant information on the evolutionary stage of a horse as do the teeth.

The taxonomy of the Equidae followed is that of Stirton (1940). Although Quinn (1955) made several alterations which should not be easily rejected, I find his extreme vertical phylogeny hard to follow in taxonomic practice.

The beds containing the fossils crop out in a band extending from the Nueces River on the west to the Sabine River on the east, and paralleling the present coastline (Quinn, 1955, p. 69, fig. 5). Quinn (pp. 69-76) discussed the biostratigraphy of the Texas Gulf Coastal Plain, and distinguished four main successive faunas, which he called, from the oldest to the youngest: the Garvin Gully, Burkeville, Cold Spring, and Lapara Creek. The

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Miocene Garvin Gully, Burkeville, and Cold Spring faunas are named after some collecting sites; the faunal names were used already by Hesse (1943, pp. 167, 170, 175). The Lapare Creek is named after the basal member of the Pliocene Goliad Formation (Quinn, 1955, pp. 69-71).

Material, Methods, Abbreviations, and Nomenclature

The material studied is in the Vertebrate Paleontology Laboratory of the Texas Memorial Museum in Austin, and in the Texas A&M University collection, part of which is on loan to the Texas Memorial Museum. It consists of isolated teeth and bones, and some jaws and skulls with teeth *in situ.* Limb bones are referred to species on the basis of size and proportions in scattergrams. There are also useful and typical morphological differences in metapodials and phalanges between, for instance, large anchitheriines and equines.

The methods used in this study are those of current standard taxonomic work. Measurements, counts, and notes were taken on isolated teeth, skulls, jaws, and limb bones, and the data handled statistically. Length and breadth of the teeth were measured at the base to avoid variation due to tapering of the crown as revealed by wear. Measurements were taken with 13 centimeter-long calipers or with a ruler, and recorded to a tenth of a millimeter. Measurements in the text are in centimeters.

The hypsodonty index is calculated as 100 x mean height of unworn or little worn teeth/mean length of the teeth.

Abbreviations used are:

AMNH	American Museum of Natural History
MCZ	Museum of Comparative Zoology
SMU	Southern Methodist University
TAM	Texas A&M University
TMM	Texas Memorial Museum
UCMP	University of California, Museum of Paleontology
GG	Garvin Gully
B	Burkeville
CS	Cold Spring
LPC	Lapara Creek
ThF	Thomas Farm fossil fauna, Thomas Farm, Gilchrist Co., Fla.
M	mean (in tables)
OR	observed range
N	number of observations
σ	standard deviation
V	coefficient of variation
M	molar (in text)
P	premolar
D	deciduous tooth
R	right
L	left
l.	length
br.	breadth
ap	anteroposterior diameter

The nomenclature of the horse teeth is according to Stirton (1940) as used by Quinn (1955). The volar ligamental scars of the first and second medial phalanx are according to Camp and Smith (1940).

Acknowledgments

This work was done when visiting the University of Texas at Austin as post-doctoral fellow 1970-71. I am thankful to Dr. John A. Wilson for sponsoring this work, for his suggestions and discussions, and to Drs. Wilson, Wann Langston, and Ernest Lundelius of the University of Texas and Texas Memorial Museum for allowing me to use their private libraries. My thanks are also due Professor Bryan Patterson of the Museum of Comparative Zoology at Harvard University, Dr. Thomas Patton of Florida State Museum of the University of Florida, and Mssrs. Stephen Windham and C. W. Hendry, Jr. of the Florida Geological Survey, for allowing me to study the Thomas Farm collections in their care. I studied comparative material from the Clarendonian and Hemphillian of Texas in the collections at Midwestern University, West Texas State University, and the Panhandle-Plains Historical Museum, and I thank Drs. Walter W. Dalquest and Gerald Schultz for their great helpfulness. The Burge and Minnechaduza samples, recently described by Webb (1969), are in the Museum of Paleontology of the University of California at Berkeley, and are here referred to. I also studied samples of fossil horses in the University of Nebraska State Museum. My gratitude is due to Drs. Donald E. Savage and Bertrand Schultz, and Mssrs. Tom Williams, King Ritchey, and Lloyd Tanner. Dr. Bjorn Kurtén of the Department of Zoology at the University of Helsinki read the manuscript, for which I am grateful.

SYSTEMATIC DESCRIPTION

Order PERISSODACTYLA Owen, 1841
Suborder HIPPOMORPHA Wood, 1937
Family EQUIDAE Gray, 1821
Subfamily ANCHITHERIINAE Osborn, 1910
Genus *Archaeohippus* Gidley, 1906

Genotype: *Anchitherium ultimum* Cope, 1886

Archaeohippus blackbergi (Hay), 1924
Tables 1, 2, 3, 24; Figs. 1, 2

Miohippus blackbergi Hay, 1924
Parahippus minutalis Hay, 1924
Archaeohippus nanus Simpson, 1932
Miohippus sp. White, 1942

Type. L upper molar (Hay, 1924, pl. 1, figs. 4, 5) in the Texas A&M University collection, from GG, Grimes Co., Texas.

Occurrence. GG fauna, Lower Hemingfordian of Texas Gulf Coastal Plain; also ThF and Midway faunas of Florida, and Flint Hill fauna of South Dakota.

Material. TMM 31084, GG, Grimes Co.: No. 98 L upper M or P; TMM

TABLE 1.–TEETH MEASUREMENTS, *ARCHAEOHIPPUS BLACKBERGI*, GG

Number (TMM)	31084-98	31259-1	40067-62	40067-121	40067-36
Tooth	L$^{P \text{ or } M}$	R$^{P \text{ or } M}$	L$^{P \text{ or } M}$	LM^3	R^D
Length	+0.87	0.93	0.87	0.89	1.06
Ant. br.		1.20	1.17	1.00	1.05
Post. br.				0.95	
(TMM)	40106-58	40106-52	40106-53	40106-60	40106-71
Tooth	L$_P$	L$_D$	L$_M$	LM^3	L^D
Length	1.00	1.08	1.03	0.95	0.99
Ant. br.	0.84	0.74	0.82	1.12	
Post. br.	0.83	0.70	0.76	1.03	
(TMM)	40106-6	40106-30	40106-32	40106-11	40106-2
Tooth	RD^2	RM$_3$	R$^{P \text{ or } M}$	L$^{P \text{ or } M}$	LM^3
Length	1.21	1.10	1.01	1.00	0.97
Ant. br.	1.09	0.58		1.23	1.13
Post. br.	1.13	0.50			
(SMU)	62429	62429	62429	62429	62429
Tooth	LP$_3$	LP$_4$	LM$_1$	LM$_2$	LM$_3$
Length	1.00	1.00	0.94	0.95	1.19
Ant. br.	0.78	0.86	0.79	0.78	0.78
Post. br.	0.83	0.84	0.74	0.71	0.58

31259, Rocky Creek at Hwy 71: No. 1 R upper M or P; TMM 40067, Hidalgo Bluff, Washington Co.: Nos. 36, 37 R and L upper D, 62 L upper P or M, 121 L M^3, 69 distal metapodial, 116, 119 L MC III, 122 distal tibia, 183 astragalus, SMU 62429 L ramus with P$_3$-M$_3$; TMM 40106, Farm Road 244, Grimes Co.: Nos. 2, 60 2L M^3, 6 R D^2, 7, 52, 71 3L upper D, 11, 32 L and R upper P or M, 30 R M$_3$, 53, 58 L lower M and P, 15 astragalus, TAM (no number) 9 astragali, 2 prox. MT III, 2 dist. metapodials (locality reference uncertain).

Diagnosis. Small, brachyodont. Upper cheek teeth with metaloph connected to ectoloph, or occasionally disconnected. Marked protoconule, slight or submerged metaconule. Crochet variable, disconnected or rarely connected to protoloph in deciduous teeth; additional plications on metaloph rare. Anterior cingulum well developed, slight lingual cingulum. Lower cheek teeth with metaconid and metastylid usually separated. Anterior and posterior cingulum; labial cingulum variable. Cement rare. M^3_3 reduced relative to M^2_2.

Description. Teeth of this small species are not well represented in the GG fauna, but there are a number of limb bones which can be referred to *A. blackbergi.* I have not seen the types of *Miohippus blackbergi* and *Parahippus minutalis,* which are missing in the TAM collection.

White (1942) referred *A. blackbergi* to the genus *Parahippus* and Bader (1956) left it there, but Quinn (1955) placed it back in Gidley's genus *Archaeohippus,* where I believe it belongs.

Hay (1924) described teeth of *M. blackbergi* and *P. minutalis* as having the protoloph and metaloph connected to the ectoloph, prominent styles and ribbing of the ectoloph, triangular hypostyle, and lacking a lingual cingulum. In the upper deciduous teeth the lingual cingulum is sometimes faintly developed. According to Hay the protoconule is swollen in *M. blackbergi,* but only slightly constricted from the protocone in *P. minutalis.* I have not observed a single isolated protocone in the permanent teeth, but in the unworn or slightly worn deciduous teeth the protocone is frequently disconnected. The metaconule is described as submerged in *M. blackbergi,* constricted from the hypocone in *P. minutalis.* In upper deciduous teeth the metaconule is somewhat more strongly marked than in permanent teeth; sometimes also molars and premolars differ in this respect, the molars being more lophodont than the premolars.

Hay placed the teeth with a crochet (with one exception) in the species *P. minutalis,* and the ones without a crochet in *M. blackbergi.* In the material at hand the crochet is variable, but is more frequent in M^3 and upper deciduous teeth than in permanent P^3-M^2. Additional plications along the metaloph are very infrequent; Hay described them as absent, and I observed only one specimen, an M^3, with a small additional plication on the posterior side of the metaloph.

TABLE 2.–DEVELOPMENT OF THE CROCHET, *ARCHAEOHIPPUS BLACKBERGI,* ThF

Tooth	Crochet	No Crochet	Total	% Crochet
P^2	5	46	51	9.8
P^3-M^2	103	120	223	46.19
M^3	38	22	60	63.3
D^2	2	8	10	20
D^3-D^4	9	16	25	36

TABLE 3.–STATISTICS OF THE TEETH, *ARCHAEOHIPPUS BLACKBERGI,* ThF

Variate	N	M	σ	V	OR
P^3-M^2 length	206	1.08±.004	0.063	5.89	0.93- 1.25
Ant. br.	168	1.37±.005	0.070	5.11	1.14- 1.57
Post. br.	148	1.34±.005	0.058	4.35	1.18- 1.46
P_3-P_4 length	100	1.06±.006	0.061	5.82	0.93- 1.25
Ant. br.	100	0.79±.007	0.067	8.39	0.67- 0.98
Post. br.	101	0.84±.006	0.059	6.96	0.69- 0.99
M_1-M_2	131	1.00±.005	0.055	5.51	0.82- 1.12
Ant. br.	130	0.79±.004	0.049	6.11	0.66- 0.90
Post. br.	127	0.74±.005	0.055	7.46	0.58- 0.87

Hay described lower cheek teeth only in *M. blackbergi*, and observed a labial cingulum, slight cement, and lack of a separating groove between the metaconid and metastylid. In my material a cingulum is absent or is only faintly developed labially, and I consider the metaconid and metastylid well separated. I have not observed cement in a single upper or lower tooth.

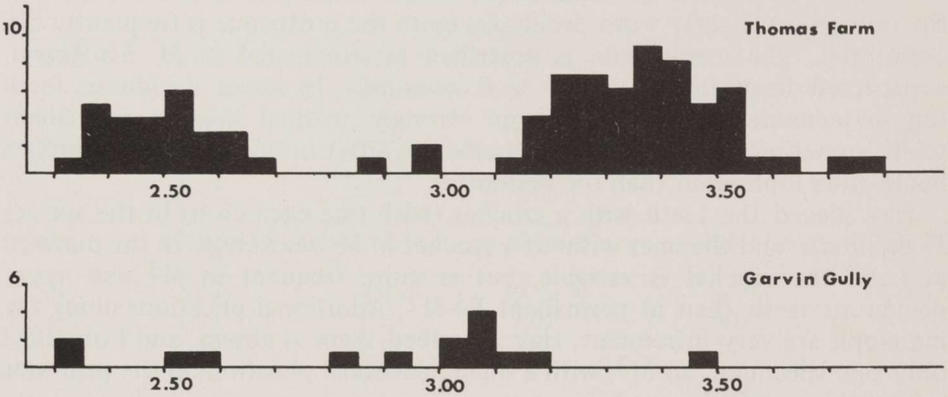

Fig. 1.—Frequency distributions of distal breadth of tibia in the samples from GG and ThF. Vertical scale: number of observations; horizontal scale: distal breadth of tibia. There is partial overlap between the measures for *Parahippus leonensis* (to the R), and complete overlap between the measures for *Archaeohippus blackbergi* (to the L).

Limbs. A number of limb bones can be referred to this small species. The metapodials are similar to those of *Parahippus leonensis*, but the distal keel is confined almost wholly to the posterior half of the distal articular surface. The proximal facet for the cuboid is slanting posteriorly, and there is no facet for the mesocuneiform.

Phalanx 1 is small and narrow. The sesamoidean and volar ligamental scars are usually well visible. The cruciate ligaments leave short, broad scars which converge toward each other, but fail to meet. The central ligament leaves a round or oval scar close to and distal from the cruciate scar. The lateral volar ligaments almost always leave scars, and in some specimens there are faint indications of paried central volar ligamental scars.

In the second medial phalanx the volar proximal shelf, on which insert the superficial sesamoidean ligament and strands of the flexor sublimis, is narrower than in the advanced horses. The superficial sesamoidean ligament was probably not developed, as is presumably the case in earlier equids including *Mesohippus* (Camp and Smith, 1942), or was only incipient. The rounded scars in this area are probably for median and lateral strands of the flexor sublimis tendon, and for the paired central volar ligaments.

Discussion. Stirton (1940) listed both *Archaeohippus blackbergi* and *A. minutalis*, but tentatively synonymized them in the text (p. 176). He also listed *A. nanus* Simpson. White (1942) synonymized *A. nanus* and *A. blackbergi*, and Bader (1956) and Downs (1956) concurred. Quinn (1955, p. 13), on the other hand, found little overlap in size of these forms and considered them distinct. Using all data available on *A. blackbergi* from GG it is evident

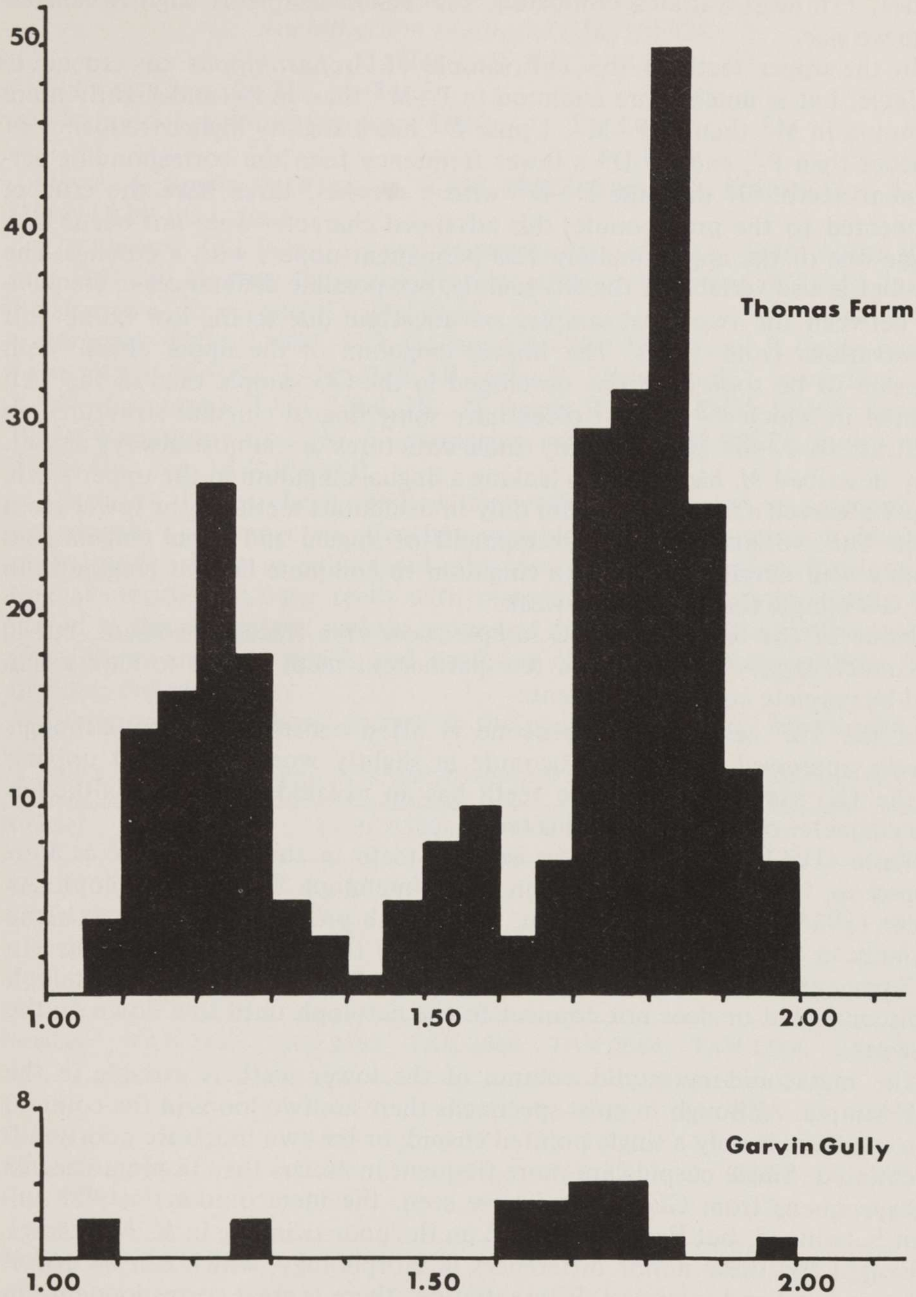

Fig. 2.–Frequency distributions of distal breadth of MT-MC III in the samples from GG and ThF. There is complete overlap of the distributions of *P. leonensis* (on the R), and *A. blackbergi* (on the L).

that the samples from GG and ThF do overlap in size of the teeth and limb bones; for most variates compared, the Texas sample is slightly smaller in mean size.

In the upper teeth of the ThF sample of *Archaeohippus* the crochet is variable, but is much more common in P^3-M^3 than in P^2, and slightly more common in M^3 than in P^3-M^2. Upper D^2 has a slightly higher frequency of crochet than P^2, and D^3-D^4 a lower frequency than the corresponding permanent teeth. Of the nine D^3-D^4 with a crochet, three have the crochet connected to the protoconule; this advanced character does not occur in a single one of the approximately 150 permanent uppers with a crochet. The crochet is also variable in the GG sample, but possible differences in frequency between the two local samples are uncertain due to the low number of observations from Texas. The lingual cingulum of the upper cheek teeth appears to be somewhat less developed in the GG sample than in the ThF sample in which P^2 and M^3 often have some lingual cingular structures, in contrast to P^3-M^2 in which any such structures are almost always absent. Hay described *M. blackbergi* as lacking a lingual cingulum in the upper teeth, and I observed a lingual cingulum only in deciduous teeth. In the lower teeth from ThF, variation in the development of lingual and labial cingula goes from a well developed shelf-like cingulum to complete lack of cingulum. In the GG sample the cingulum is weak.

None of the teeth in the GG sample show even traces of cement, but in the much larger ThF sample a few permanent teeth appear to have a thin and incomplete coating of cement.

In the ThF sample the protocone is often constricted from, although closely appressed to, the protoconule in slightly worn permanent uppers; in the GG sample none of the teeth has an isolated protocone, although this character occurs in deciduous teeth.

White (1942) identified a few isolated teeth in the ThF sample as *Miohippus* sp. because of the isolation of the metaloph from the ectoloph. As Bader (1956) already pointed out, these teeth probably represent extreme deviants in *Archaeohippus,* or phenocopies of the more primitive genus. In 6–7 percent of P^3-M^2, 14 percent of M^3, and 17 percent of P^2 the metaloph is disconnected or does not connect to the ectoloph until low down on the crown.

The metaconid-metastylid column of the lower teeth is variable in the ThF sample. Although in most specimens there are two loops in the column, in some there is only a single pointed cuspid, or the two loops are poorly differentiated. Single cuspids are more frequent in molars than in premolars. In the specimens from GG which I have seen, the metaconid-metastylid column is twinned, but Hay commented on the poor twinning in *M. blackbergi.*

Except for these minor differences in morphology, which can be understood as local and temporal differentiation, there is great correspondence in size and proportions, and morphology of the teeth and limb bones in the samples from GG and ThF. The two samples should certainly be regarded as drawn from a widely dispersed population of one species.

Genus *Anchitherium* v. Meyer, 1844

Genotype: *Palaeotherium aurelianense* Cuvier, 1825

Anchitherium navasotae (Hay), 1924

Tables 4, 25; Fig. 3

Miohippus navasotae Hay, 1924
Anchitherium clarencei Simpson, 1932

Type. L upper third molar, TAM 2385, from GG, Grimes Co., Texas (Hay, 1924, pl. 1, fig.).

Occurrence. GG fauna, Lower Hemingfordian of Texas Gulf Coastal Plain and ThF and Midway faunas of Florida; referred "younger" B fauna, Lower Barstovian of Texas Gulf Coastal Plain.

Material. TMM 31084, GG, Grimes Co.: No. 137 L and R upper molars (cast UCMP 35604), TAM 2385 3R lower P, 2R lower M, L lower D, L M$_3$, L M^3 (holotype), TAM 2564 2R, 2L upper P or M; TMM 40067, Hidalgo Bluff, Washington Co.: No. 57 astragalus; referred TMM 40623, Push Creek, Tyoer Co.: No. 13 R lower P.

Diagnosis. Upper cheek teeth with metaloph connected to ectoloph, or occasionally disconnected. Crochet variable, rare, disconnected. Marked protoconule; slight or submerged metaconule. Broad anterior cingulum, no lingual cingulum. Lower teeth with metaconid and metastylid slightly separated in the premolars; slightly separated or undifferentiated in the molars. Continuous anterior, labial, and posterior cingulum; lingual cingulum faint or none. No cement.

Description. This horse is rare in the material from GG. I have seen the

TABLE 4.–TEETH MEASUREMENTS, *ANCHITHERIUM NAVASOTAE*, GG AND PUSH CREEK

Number	UCBC 35604	UCBC 35604	TAM 2585	TAM 2385	TAM 2385
Tooth	L^M	R^P or ^{M}	LM^3	R$_p$	R$_p$
Length	1.80	±2.00	1.60	1.85	1.80
Ant. br.	2.40		2.07	1.24	1.39
Post. br.				1.39	1.42

Number	TAM 2385	TAM 2564	TAM 2564	TAM 2564	TAM 2564	TAM 2564
Tooth	L$_D$	R$_p$	R$_p$	R$_M$	R$_M$	LM$_3$
Length	2.03	1.91	1.91	1.77	1.72	
Ant. br.	1.32	1.25	1.25	1.35	1.22	1.15
Post. br.	1.40	1.50	1.50	1.15	1.15	0.98

Number	TMM 40623-13
Tooth	R$_p$
Length	1.91
Ant. br.	1.40
Post. br.	1.53

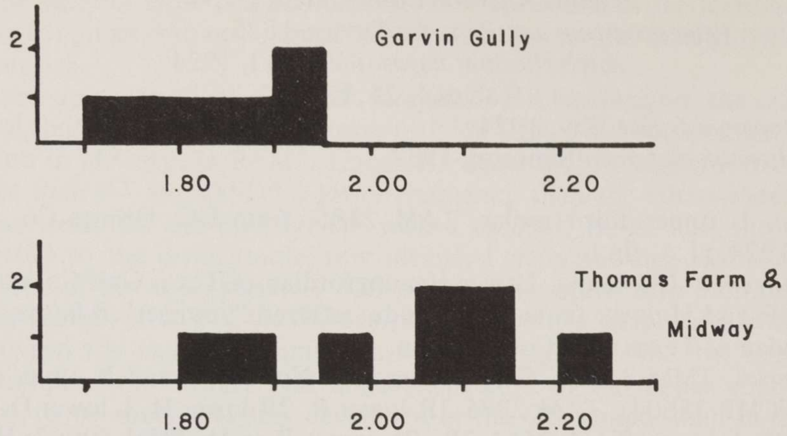

Fig. 3.—Frequency distributions of length of P_3-M_2 in samples of *Anchitherium navasotae* from GG and ThF (data on *Anchitherium* from ThF partly from Simpson 1930, 1932). The mean for the GG sample is slightly less than for the ThF sample.

type and hypodigm of *Miohippus navasotae* described by Hay (1924), and a few additional specimens in the Texas A&M University collection and the Museum of Paleontology, University of California at Berkeley.

The ectoloph is flat or very faintly ribbed. There is a broad labial cingulum and prominent parastyle and mesostyle. The parastyle is flat or broadly rounded; it is slightly grooved at the top. The mesostyle is pointed. The protoloph connects low to the ectoloph; the metaloph is connected or seldom disconnected. The crochet is variable.

The protoconule is slightly swollen, but not sharply constricted from the protocone, which is transversely broad, oval, and connate, and reaches labially the base of the paracone. The metaloph is lophoid; the metaconule is submerged. The hypostyle is triangular, encloses a fossette and connects low to the metaloph. There is a broad, shelf-like anterior cingulum between the protocone and protoconule, usually continuous to the parastyle. There is a slight posterior, but no lingual cingulum.

In the lower cheek teeth the metaconid-metastylid loops are separated by a short lingual groove in beginning of wear. Usually there is a continuous anterior, labial, and posterior cingulum, but no lingual cingulum or very faintly developed in the entrants of the flexids.

Discussion. These teeth differ from teeth of *Parahippus* in the lack of, or very slight ribbing of the ectoloph, more lophoid protoloph and metaloph, shelf-like, broad anterior cingulum, transversely much broader protocone, and lack of cement. Astragalus is heavier and larger than any other specimen in the sample from GG.

Hay (1924) described *M. navasotae* from GG on the basis of one upper and three lower cheek teeth. He noted disconnected lophs, slight development of the conules and crochet, and indication of cement in this species. In the type upper M^3 (TAM 2385) the metaloph does not reach the ectoloph, but from the ectoloph a plate-like projection (broken in the specimen) reaches out toward the metaloph. There is a minute crochet, which in another specimen (TAM 2564) is better developed. What Hay believed to be cement is probably only a discoloration of the enamel, not a true depositionary layer.

In describing the lower cheek teeth Hay commented on the faint separation of the loops of the metaconid-metastylid, although he described a deciduous tooth (Hay, 1924, pl. 1, figs. 11, 12) as a lower molar with well separated loops. There is no cement on the lower teeth.

The teeth and the astragalus (TMM 40067-57) from GG compare closely in morphology with the material from Florida (Thomas Farm and Midway) described by Simpson (1932) as *Anchitherium clarencei.* Astragalus from GG is almost exactly the size of MCZ 7597 of the hypodigm of *A. clarencei,* but the teeth are slightly smaller. Both forms belong among the smallest of the genus *Anchitherium* in North America.

The type M^3 of *M. navasotae* is not as reduced as M^3 in the type of *A. clarencei;* although the protocone is considerably larger than the hypocone, neither M^3 is triangular. In the only M_3 from GG, unfortunately the hypoconulid is missing, but the tooth does not appear to be reduced in comparison to lower first and second molars in the sample. Simpson (1932) compared *A. clarencei* with *"Kalobatippus" (Anchitherium) agatensis,* and concluded that the former species has a more reduced M^3_3 and a better developed hypostyle. He also thought that *A. clarencei* differed from Old World *Anchitherium* in the absence of a lingual cingulum. There is little difference in the morphology of the teeth of *A. agatensis* and *A. clarencei,* although the length of M^3_3 compared to the length of the corresponding M^2_2 is reduced in the latter; in this respect, *A. clarencei* resembles species of the genus *Hypohippus* more than *"Kalobatippus."* The metapodials of *A. clarencei* are shorter and relatively stouter than those of *"Kalobatippus;"* this is also a character in common with *Hypohippus* and Old World *Anchitherium.* On the other hand, European *Anchitherium* has no better developed a lingual cingulum than *A. clarencei;* in both there is considerable variation.

In view of the slight differences between the samples from GG and ThF, I am inclined to regard the two species as synonymous, although Stirton (1940, p. 174) listed both. *Anchitherium navasotae* is the earliest valid name.

In the material from Push Creek, Tyler County, Texas, there is a lower cheek tooth (TMM 40623-13) of an anchitheriine horse. *Anchitherium* is not found at any site in the B or CS; at Push Creek this genus occurs together with a large *Parahippus* and *Merychippus vetus.* The Push Creek fauna is little known and according to Wilson (in letter), *Anchitherium* may be reworked.

The metaconid and metastylid are faintly separated by a short lingual groove. The entoconid is large and rounded, and there is a well defined hypoconulid. The anterior, labial, and posterior cingulum is continuous; there is no lingual cingulum, but some low stylids in the entrants of the flexids.

This tooth agrees completely in size and morphology with specimens in the GG sample.

Genus *Hypohippus* Leidy, 1858

Genotype: *Hypohippus affinis* Leidy, 1858

Hypohippus affinis Leidy, 1858

Tables 5, 26

Type. L upper deciduous third or fourth molar, U. S. National Museum No. 573, Washington D. C., from Ft. Niobrara, Nebraska.

Occurrence. Lapara Creek fauna, Clarendonian of Texas Gulf Coastal Plain and Texas Panhandle; Barstovian to Clarendonian of Great Plains.

Material. TMM 31132, Site 17, Bridge Farm, Bee County: No. 447 R P_2, 75 R astragalus; TMM 30936, Site 8, George West, Live Oak County: No. 348 L D^2; TMM 41040, 7 mi. S. Hallettsville on road to Victoria: No. 1 R lower P or M.

Diagnosis. Leidy (1858), according to Gidley (1907), revised: cheek teeth brachyodont, lophodont. Uppers with metaloph united to ectoloph, slight protoconule, metaconule submerged; protocone and hypocone large, conical; paracone and metacone concave, no ribbing; crochet variable, disconnected; hypostyle variable. Lowers with metaconid and metastylid divided by a notch in the premolars, barely divided or undivided in the molars. Cingulum variable, cement none. M^3_3 relatively reduced.

TABLE 5.–TEETH MEASUREMENTS, *HYPOHIPPUS AFFINIS*, LPC

Number	TMM 41040-1	 31132-447	 30936-348
Tooth	R^P or ^{M}	RP_2	LD^2
Length		2.51	3.08
Ant. br.		1.15	2.48
Post. br.	2.10	1.51	

Description. Only a few teeth indicate the presence of this large anchitheriine in the LPC.

Lower P_2 (TMM 31132-447): Incipient budding off of metaconid, but no lingual groove between the cuspids. Well developed hypoconulid and anterior continuation of paralophid. Cingulum developed posteriorly; slight cingulum between conids and anterior of paralophid.

Upper D^2 (TMM 30936-348): Protoloph disconnected, metaloph connected. Crochet. Protoconule marked, but small; metaconule submerged. Large, triangular hypostyle enclosing lake. Broad, shelf-like anterior cingulum; slight cingular style between protocone and hypocone, and slight posterior cingulum.

Discussion. I compared D^2 from LPC with a juvenile skull with R and L D^2-D^4 (TMM 40282-3) from the Clarendon of "N of S fork of Red River," Donley County, Texas. Cope described and figured this skull as *Pliohippus pachyops*, but it is not the holotype of that species. Gidley (1907, pp. 913-914) identified it as *Hypohippus affinis*, and remarked on the close resemblance in size to the type of that species, a deciduous D^3 or D^4. Upper D^2 from LPC is almost identical to D^2 in the Clarendon skull.

The measurements on the scant *Hypohippus* material from Texas agree well with data on referred material of *H. affinis.* The teeth are slightly larger than those from Burge, and usually fall in between specimens of *H. affinis* from Burge and specimens referred to *H. nevadensis.* One astragalus (TMM 31132-75) is smaller than a specimen of *H. affinis* from Gordon Creek (Burge l.f.) (UCB 35463), but is the size of astragalus (Univ. Colorado Museum No. 31611) from Verdigre, Nebraska.

In the LPC is a fragment of a permanent lower tooth (TMM 41040-1) which, although very large, still is inside the range of variation of *H. affinis.* There is a complete labial cingulum, which is rather low. The geologic age of this specimen is somewhat uncertain, but its large size would place it close to the LPC and Clarendon specimens in time.

A fragmentary P^2 from a well at Independence, Washington County, Texas probably belongs to *H. affinis* and was described by Leidy (1873) as *Anchitherium (?) australis.* Osborn (1918) commented on the similarity of this tooth to *Hypohippus;* Stirton (1940, p. 174) listed it as *A. australis.* The large protocone and hypocone, and lophoid metaloph with submerged metaconule are features which suggest the genera *Anchitherium* or *Hypohippus* rather than *Parahippus.* The size of the specimen (+ 2.45 x 2.30) corresponds to the size of the teeth in *H. affinis.* Leidy (1973) considered the age of the fossil sample, which included the type of *A. (?) australe* and an upper tooth of *"Protohippus perditus,"* as Upper Miocene. Hesse (1942, p. 166), on the other hand, thought it to be Lower Oakville and equivalent to GG. He based his conclusion on the depth of the well from which the fossils were stated to have come, which would place them "below the base of the Moulton sandstone (= Middle Oakville) (Hesse, p. 160) in that area." The fragmentary P^2 (Leidy, 1873, pl. XX, fig. 19) of *A. (?) australe* is too large for *A. navasotae,* and Leidy's figure (1873, pl. XX, fig. 16) of the tooth of *"Protohippus perditus"* shows a worn premolar of *Protohippus* or *Pliohippus.* These horses are certainly advanced over GG *Parahippus,* and indicate an Upper Miocene (Barstovian) age as Leidy originally assumed.

Genus *Parahippus* Leidy, 1858

Genotype: *Anchitherium (Parahippus) cognatus* Leidy, 1858

Parahippus leonensis Sellards, 1916

Tables 6, 7, 9, 10, 27; Figs. 1, 2, 4

Merychippus vellicans Hay, 1924
Merychippus socius Hay, 1924
Parahippus barbouri White, 1942

Type. R upper molar, Florida Geological Survey V-5084, from Griscom Plantation, 15 mi. N or Tallahassee, Florida.

Occurrence. GG fauna, Lower Hemingfordian of Texas Gulf Coastal Plain and ThF fauna of Florida.

Material. TMM 40142, Moulton sp., Grimes Co.: (no number) L M_2-M_3;

TABLE 6.–STATISTICS OF THE TEETH, *PARAHIPPUS LEONENSIS*, GG

Variate	N	M	σ	V	OR
P^3-M^2 length	119	1.42±.008	0.085	6.01	1.21- 1.67
br.	95	1.79±.010	0.099	5.55	1.55- 2.06
P_3-P_4 length	56	1.43±.009	0.070	4.92	1.28- 1.58
Ant. br.	50	1.17±.013	0.094	8.06	0.93- 1.33
Post. br.	56	1.23±.010	0.078	6.33	1.01- 1.38
M_1-M_2 length	90	1.35±.008	0.074	5.44	1.17- 1.50
Ant. br.	87	1.11±.009	0.080	7.21	0.94- 1.45
Post. br.	87	1.02±.010	0.089	8.72	0.80- 1.29

TABLE 7.–STATISTICS OF THE TEETH, *PARAHIPPUS LEONENSIS*, ThF

Variate	N	M	σ	V	OR
P^3-M^2 length	346	1.53±.005	0.095	6.22	1.15- 1.78
Ant. br.	222	1.90±.009	0.129	6.84	1.50- 2.15
Post. br.	161	1.87±.010	0.129	6.90	1.51- 2.13
P_3-M_4 length	404	1.50±.004	0.084	5.61	1.16- 1.70
Ant. br.	387	1.25±.004	0.085	6.79	0.97- 1.42
Post. br.	378	1.28±.004	0.076	5.90	1.05- 1.45
M_1-M_2 length	395	1.41±.004	0.082	5.82	1.19- 1.62
Ant. br.	392	1.16±.004	0.081	7.00	0.92- 1.44
Post. br.	374	1.08±.005	0.088	8.18	0.82- 1.33

TABLE 8.–TEETH MEASUREMENTS,
PARAHIPPUS cf. P. TEXANUS, GG AND PUSH CREEK

Number	TMM				
	40068-7	40067-63	40623-9	40623-9	40623-9
Tooth	LM^3	RM^3	RP^2	RP^3	RP^4
Length	1.69	1.65	+ 2.15	1.75	1.66
Br.	2.30	2.00	1.87	2.07	2.13

TMM 31084, GG, Grimes Co.: Nos. 59, 92 2L lower P, 140 L lower P (cast UCMP 32603), 130 L lower M, 59 R upper P, 91, 138 2R upper P (casts UCMP 34428, 34429), 41, 109 2L upper M, 86 R upper M, 103 R M^3, 50, 101 R P^2, P^3, P^4 (cast TAM 2397, composite), 50 R P$_2$, 2 lower M, 70 R ramus with P$_2$-M$_3$ (cast TAM 2589), 139 R and L uppers and lowers (casts UCMP 32603), 30 astragalus, 42 phalanx 2, 56 distal tibia, 117, 125, 2 distal metapodials; TMM 40106, Farm Rd. 244, Grimes Co.: No. 57 L lower P, 28 R lower M, 33 R M$_3$, 5, 44 2R M^3, 73 L upper D; TMM 40067, 3 mi. N of William Penn School, Hidalgo Bluff, Washington Co.: Nos. 59, 133, 193 3R upper M, 167 L upper M, 134 L upper P or M, L lower D, 35 D^2, 149 R lower M, R M$_3$, 126 R lower M, 57, 142 2 astragali; TMM 40104, below Hidalgo Church, Washington Co.: No. 3 R lower M; TMM 40071, 1.5 mi. N of Hwy 244, Washington Co.: No. 4 R M^3, 1 astragalus; TMM 40643, Garvin Farm, Navasota, Grimes Co.: Nos. 16 L upper M (cast TAM 2396, type *M. vellicans*), L lower P, lower M, lower M$_3$ (casts), 15 L P^2, P^3 (cast TAM 2377, type *M. socius*), L upper M, M^3 (cast TAM 2377, co-type *M. socius*), TAM 2377 (original type and co-type *M. socius*), TAM 2396 (original type of *M. vellicans*), TAM 2397 R P$_2$, M and P (co-type *M. vellicans*, composite), TAM 2550 L P$_2$, P$_3$, and L uppers, TAM 2551 R uppers, TAM 2568 R symphysis and ramus with P$_2$-M$_3$, TAM 2571 isolated lowers, TAM 2571A isolated lowers, TAM 2589 R ramus with P$_2$-M$_3$ and 2 casts, TAM (no number) isolated uppers, R ramus with P$_2$-M$_3$, and various limb bones; TMM 40217, Farm Rd. 1774, 0.5 mi. E of Anderson, Grimes Co.: No. 2 astragalus.

TABLE 9.–DEVELOPMENT OF THE CROCHET, *PARAHIPPUS LEONENSIS*, GG

Wear stage	Tooth	Crochet free	Crochet connected	No crochet	Total	Percent connected	Percent no crochet
Slight	P^2	1	0	0	1	0	0
Some		6	0	1	7	0	14.3
Well		8	0	1	9	0	11.1
Much		1	1	1	3	33.3	33.3
Total		16	1	3	20	5	15
Slight	P^3-M^2	22	4	1	27	15	3.7
Some		10	0	0	10	0	0
Well		54	18	1	73	24.7	1.4
Much		14	10	0	24	41.7	0
Total		100	32	2	134	21.9	1.49
Slight	M^3	15	1	0	16	6.3	0
Some		1	0	0	1	0	0
Well		4	1	0	5	20	0
Total		20	2	0	22	9.1	0

Diagnosis. Quinn (1955, p. 13, revised): Brachyodont or subhypsodont. Premolars and molars truncate wedge-shaped with base of crowns wide and summit narrow transversely; external face of premolars slightly convex, molars slightly concave. Parastylid weak, sloping diagonally across anterior face of teeth. Metaconid and metastylid well separated, flexids shallow. Pli hypoconid. Metaloph seldom disconnected from ectoloph; crochet seldom connecting to protoloph until well worn; protocone disconnected with spur in early wear, soon connecting. Traces of internal and external cingula. Cement.

Description. This is the most common horse in the collection from GG. It is represented by teeth, jaws, and limb bones. The types and co-types (TAM 2377, 2396, and 2397) of *Merychippus vellicans* and *M. socius* are in the Texas A&M University collection.

In the upper teeth the styles are well developed, the parastyle is flattened or slightly bifurcate in the beginning of wear in P^3-M^2. The paracone and metacone are slightly ribbed in most uppers. The metaloph is usually connected to the ectoloph in the permanent uppers, although I have observed two cases of P^3-M^2 where the metaloph was disconnected, and this character is frequent in P^2.

The protoconule is constricted and the protocone is usually isolated in beginning of wear. The metaconule is slightly swollen, more so in premolars

TABLE 10.–DEVELOPMENT OF THE CROCHET,
PARAHIPPUS LEONENSIS, ThF

Wear stage	Tooth	Crochet free	Crochet connected	No crochet	Total	Percent connected	Percent no crochet
Slight	P^2	9	0	4	13	0	30.8
Some		11	0	4	15	0	26.7
Well		58	4	13	71	0	18.3
Much		11	4	4	19	21.1	21.1
Total		89	4	25	118	3.4	21.2
Slight	P^3-M^2	60	3	0	63	4.8	0
Some		61	0	0	61	0	0
Well		226	27	0	253	10.7	0
Much		44	33	5	82	42.4	6.1
Total		391	63	5	459	13.7	1.1
Slight	M^3	52	3	0	55	5.5	0
Some		8	0	0	8	0	0
Well		55	7	1	63	12.7	1.6
Much		8	2	0	10	20	0
Total		123	12	1	136	8.8	0.7

than in the molars. The crochet is mostly simple and fingerlike; in specimens with a complicated enamel pattern the crochet is bifurcate or T-shaped, seldom trifurcate. In approximately two specimens in 15 unworn or slightly worn uppers the crochet is already connected to the protoloph. In a few specimens a crochet is absent. The plications along the metaloph are variable; there are none to several anterior and posterior plications, and mostly the metaloph is simple. On the basis of the number of plications along the metaloph, different populations cannot be sorted out in the sample. Hay (1924) described *M. socius* as having a simpler enamel pattern than *M. vellicans,* but there is a complete gradation from no plications to numerous plications. A pli caballin occurs where the crochet is T-shaped.

The unworn protocone is usually oval, transversely flattened or pointed, isolated with a spur but soon connecting to the protoconule, and crescentic rounded-oval when worn. The hypocone is similar to the protocone and roughly equal in size, flattened-oval in beginning of wear, rounded-oval when worn.

Hay noted as one of the differences between *M. vellicans* and *M. socius* that in *M. vellicans* the metaloph is uninterrupted from beginning of wear, but in *M. socius* the hypocone is isolated at an early stage. In his illustrations of the types of *M. socius* (Hay, 1924, pl. 1, figs. 25, 26) only M^3 has an isolated hypocone. In the material I studied, some unworn or slightly worn M^3s evidently have an isolated hypocone as there is a shallow groove filled with cement separating the hypocone from the metaconule, but these teeth do not otherwise differ from M^3 with no separating groove.

There is a low labial cingulum and usually a cingulum anteriorly between the protocone and protoconule, sometimes forming a low style, and posteriorly between the hypocone and hypostyle. There is no lingual cingulum. The hypostyle is usually triangular, often with an enclosed lake, sometimes with hypoloph and pli dihypostyle.

In the lower cheek teeth the metaconid and metastylid are separated. In P_2 the column is simple, or there is an incipient metaconid and the loops are faintly separated. Especially unworn premolars often have a pli hypoconid in the entoflexid, and sometimes a posterior plication in the metaflexid. I have observed an entostylid, the isolated anterior tip of the entoconid in the entoflexid; with additional wear it connects to the entoconid.

The cingulum is variable; usually there is a cingulum anteriorly and posteriorly, and some cingular structures labially. Thus most teeth have a protostylid between the protoconid and hypoconid.

Milk teeth. The milk teeth resemble the permanent teeth except in proportions and height. In D^2 the protoloph may remain disconnected from the ectoloph until late wear, and the metaloph, too, is often narrowly connected. In D^3 and D^4 the transversal lophs are disconnected more often than in the permanent teeth. The hypostyle is triangular, with an open or closed fossette, and often the hypoloph is quite complicated with 2–3 plications toward the post fossette. The metaloph is also plicated. In one specimen (TAM 2551) the crochet is connected to the protoconule already in early wear; usually this connection is not formed until the tooth is well worn. The protocone and hypocone are narrowly connected to, or almost isolated from, the protoconule and metaconule in early wear. Upper D^3-D^4 have slight cingular structures lingually between the protocone and protoconule, and between the protocone and hypocone.

In the lower milk teeth the anterior cingulum is well developed as a narrow shelf almost surrounding the protoconid, and running up the low anterior wall of the paralophid. There is a low protostylid, and posteriorly a ridge runs up the hypoconulid.

The teeth are well cemented, and the milk teeth may have a thin coating of cement, as in TMM 40106-73.

Limbs. Parahippus leonensis is a middle-sized horse with slender limbs. The third metatarsals lack a proximal facet for the mesocuneiform, and the sagittal keel on the distal articular surface is only faintly developed anteriorly.

The proximal medial phalanx is slender with short scars for the cruciate ligament often meeting at the midline, short or long central, and lateral volar scars. As in *Archaeohippus blackbergi* there are occasionally scars showing the presence of central volar ligaments. As is the case in *A. blackbergi* the superficial sesamoidean ligament appears to have been only incipient. There are large insertion areas on the second medial phalanx for strands of the flexor sublimis tendon; a crescentic area between or behind these in some specimens may be the insertion of the superficial sesamoidean ligament. The ThF sample of first and second medial phalanges is unusual in its large size and in the frequent occurrence of exostotic specimens.

Discussion. Hay (1924) separated the two species *M. vellicans* and *M. socius* on the basis of minor morphological traits, which clearly are variants in a continuous series. Hay also pointed out differences in hypsodonty, but this is probably due to differences in absolute size between the teeth which he described as belonging to each species. The type teeth of *M. socius* (TAM 2377) are among the smallest in the sample, and the type (TAM 2396, and co-type 2397) of *M. vellicans* among the largest; a height difference of the type teeth then is to be expected. Stirton (1940) cited both species under *Parahippus,* but added in a footnote (p. 177) that they are synonyms.

White (1942) synonymized *P. vellicans* and *P. leonensis* Sellards from ThF, a conclusion with which Downs (1956) concurred. Quinn (1955), on the other hand, thought *P. vellicans* to be specifically distinct from the Florida form. Undoubtedly there are close similarities in morphology and size; the Texas form, however, is smaller in all variates compared.

There have been differing opinions whether the *Parahippus* sample from ThF is taxonomically homogeneous. Sellards (1916) and Simpson (1932) recognized only one species, *P. leonensis,* but White (1942) recognized three species: *P. barbouri, P. leonensis,* and *Merychippus gunteri.* The two first named he separated mainly on the basis of size, the two latter on the basis of the evolutionary stage of the morphology of the cheek teeth. Downs (1956) found little difference between *P. barbouri* and *P. leonensis,* and Bader (1956) synonymized all three species. Bader's quantitative study of the horses from ThF is the most thorough work done on the sample. Bader explained the variation in size and morphology as being due to sampling from successive temporal strata, reflecting a gradual shift in evolution in one continuous population from the small *P. "barbouri"* to the advanced *P.*

leonensis, with many individuals in the latter showing characters of primitive *Merychippus*, *M. gunteri*. Statistics on the cheek teeth do not indicate higher variation in *P. leonensis* than in *A. blackbergi* from the same site. In Bader's scattergrams, however, it is evident that whereas in *Archaeohippus* the observations cluster more or less around the mean, in *P. leonensis* the scatter is drawn out. In the frequency diagrams this is reflected in *Archaeohippus* having an almost perfect, bell-shaped distribution of the observations, whereas the distribution in *P. leonensis* begins with a slope, then reaches a peak and quickly drops off. This, Bader explained, may be due to centripetal selection in *Archaeohippus* tending to concentrate the population around the mean, and resulting in the species remaining conservative throughout the sequence. In *P. leonensis*, on the other hand, there was strong linear selection resulting in noticeable directional evolution and change of the population mean.

I repeated Bader's work and studied the sample of horses from ThF since they are the closest relatives of the GG forms. In all scattergrams the drawn-out distribution of the observations on *P. leonensis* is evident. In the case of length–breadth of long-bones such as metapodials, the scatter is not a simple one, as when all observations fall along a single axis, but there are two parallel scatters indicating differences in size and in proportions. In the frequency diagram on distal breadth of pooled MC and MT this is reflected in two closely appressed, but partly distinct peaks. The observations on *P. leonensis* from GG usually fall in among the small specimens of ThF *P. leonensis*, or, as in the case of the metapodials, fall in between the relatively narrow and broad specimens of that sample.

The teeth from ThF differ from those from GG in the more complicated crochet, which connects to the protoconule at a later stage of wear. In only three of the unworn or slightly worn P^3-M^2 from ThF which I have seen, is the crochet connected. In M^3 the crochet is as often connected in early wear stages in both samples. The total frequency of the connected crochet is significantly higher in P^3-M^2 from GG than ThF. Crochets are absent as often in both samples: P^2, 15 percent, P^3-M^2, 1.5 percent lack a crochet.

In both samples the metaloph is occasionally disconnected from the ectoloph or barely connects to a short plication reaching lingually from the ectoloph. The frequency of the disconnected metaloph is low in P^3-M^3 (1–2 percent); in P^2 it is high, especially in little-worn specimens. The samples do not differ in this character. *Parahippus leonensis* differs from *A. blackbergi* in lower frequency of disconnected metaloph in P^3-M^3, but higher frequency in P^2. Protoconal length and plication frequency are the same in the two samples of *Parahippus*. White (1942) observed a thin coating of cement in the milk teeth, and this is true also in the GG sample.

Parahippus leonensis from GG, thus, does not appear to be more primitive in tooth morphology than *P. leonensis* from ThF, only smaller. The differences between the samples suggest a geographical difference between more or less contemporaneous populations of one species, or a size difference between a closely related ancestral and descendant form.

Parahippus cf. *P. texanus* (Leidy), 1868

Tables 8, 28

Anchippus texanus Leidy, 1868

Type. L upper molar, Acad. Nat. Sci. Philadelphia collections, from Washington County, Texas.

Occurrence. GG fauna, Lower Hemingfordian of Texas Gulf Coastal Plain; referred "younger" B fauna, Lower Barstovian of Texas Gulf Coastal Plain.

Material. TMM 40068, Cedar Creek, Washington County: Nos. 7 L M^3, 18 calcaneum, 5 L proximal MT III; TMM 40067, Hidalgo Bluff, Washington County: No. 63 R M^3; TMM 40106, Farm Rd. 244, Grimes County: No. 63 R astragalus. Referred TMM 40623, Push Creek, Tyler County: No. 9 maxillar fragment with R P^2-P^4.

Diagnosis. Large, brachyodont. Metaloph connected to ectoloph; protoconule marked, metaconule marked or submerged; crochet simple, disconnected. Anterior cingulum, no lingual cingulum. Cement scarce or none.

Description. Two upper teeth, probably M^3, in the GG fauna differ from teeth of *Parahippus leonensis* in their more primitive morphology and larger size.

The ectoloph has a broad, flat or slightly grooved parastyle; the mesostyle is pointed. There is noticeable ribbing, especially of the paracone. In the protoloph the protoconule is constricted from the protocone by anterior and posterior grooves, but does not appear to be separated even in beginning of wear. Protocone and protoconule of roughly equal size; protocone slightly crescentic. The protoloph connects low to the ectoloph.

The metaloph also connects to the ectoloph, and the crochet is simple and connects low if at all to the protoloph. There are no additional plications. The metaconule is submerged, but both specimens are molars which tend to have a less developed metaconule than the premolars.

The hypostyle is triangular and notched posteriorly; it connects to the metaloph by a ridge. There is a slight anterior cingulum between the protocone and protoconule, but no posterior cingulum. The labial cingulum is complete but low. There is no lingual cingulum.

The protocone is centrally situated and larger than the reduced hypocone, giving the tooth a subtriangular outline.

Cement is thin or lacking, and there is faint striation of the enamel wall.

Discussion. In anteroposterior length these specimens fall at the $M \pm 3\sigma$ limit of *P. leonensis* from GG; in breadth they fall well outside three standard deviations from the mean of the smaller species. The most noticeable differences in morphology are in the scant development or lack of cement, and in the lack of plications on the metaloph in the larger teeth. Also the protocone appears more closely connected to the protoconule. The main difference is in size, since there are teeth of the smaller species which lack a crochet, lack cement or have a disconnected metaloph, all of which are primitive features of the teeth.

Parahippus cf. *P. texanus* differs from *Anchitherium navasotae*, which it approaches in size, in greater height of the teeth, in the form and extent of the protocone, and in the lack of a strong anterior cingulum.

In 1868 Leidy described an upper molar from Hutchen's Well, Washington County, Texas, which he called *Parahippus (Anchippus) texanus.* This tooth, figured in Osborn (1918, fig. 59), is about the size (length approx. 1.88, Princeton Museum 12187 cast) of the large *Parahippus* teeth from GG, and slightly larger than any of the teeth of *P. leonensis.* The type of *P. texanus* differs from the two teeth of *P.* cf. *P. texanus* in that the protocone is separated from the protoconule, and that the anterior cingulum is broad and shelf-like and almost surrounds the protocone. The former character is typical of many *Parahippus,* the latter of *Anchitherium* and *Hypohippus.*

Parahippus cf. *P. texanus* also resembles *P. tyleri* from Nebraska in size of teeth, in the slight development of cement, and notching of the hypostyle. The simple crochet and lophodont metaloph of *P. tyleri* are additional similarities.

In the collection from Push Creek, Tyler County, is a maxillary fragment (TMM 40623-9) belonging to a large *Parahippus.* The Push Creek fauna has been identified as CS on the basis of the occurrence there of a mastodont (Wilson, pers. comm.). *Parahippus* and *Anchitherium,* which also appear in the Push Creek, have not been found at any site in the B, nor have they been found at any other site in the CS. *Anchitherium* is undistinguishable from *A. navasotae,* and the merychippine horses in the Push Creek resemble *M. vetus, M. gunteri,* and *M.* sp.

Parahippus from Push Creek is not an advanced form of the genus, as can be inferred from the failure of the metaloph to reach the ectoloph, and the lack of a crochet. The premolars are well worn, but appear to have been brachyodont. Pd^1 was worn flat. The teeth are inserted by long roots. In P^2 and P^3 the protoloph is barely connected to the ectoloph, in P^4 the protoloph is still disconnected. In all premolars the metaloph fails to reach the ectoloph, which in P^3 and P^4 sends a short plication to meet the metaloph. The parastyle is broad, but neither the parastyle nor the metastyle is as well constricted as in *P. leonensis.* The paracone is ribbed at the top; the metacone is nearly flat.

The protoconule is prominent and round, and anteriorly sharply constricted from the protocone. The protocone is drop-formed and turns slightly anteriorly at this stage of wear. The metaconule is only little swollen and marked off from the hypocone; the metaloph is lophoid. There is no crochet, but from one to several short crenulations can be seen along the anterior border of the metaloph, and one short plication on the posterior border.

The hypostyle is triangular and connected to the hypocone. In P^2 the hypostyle encloses a minute lake.

There is a rather prominent anterior cingulum between the protocone and protoconule, but no lingual cingulum. Cement is absent on the outer walls of the teeth, but is deposited in the fossettes.

These teeth could be mistaken for deciduous teeth of *Merychippus vetus* in this fauna, but the well developed roots, the absence of any evidence of replacement teeth in the jaw, and the square shape of the teeth show that they represent permanent teeth. The specimens cannot be confused with *Anchi-*

therium or *Hypohippus* because of the structure of the lophs, especially the small protocone and pronounced protoconule, and the faint development of cingula.

The measurements on P^3 and P^4 fall outside or barely inside the M ± 3σ range of *P. leonensis*, but P^2 is much larger than any specimens from GG. There are similarities in size with *P. leonensis* from ThF, but *Parahippus* from Push Creek is more primitive. *Parahippus* from Push Creek differs from *P.* cf. *P. texanus* from GG in plications of the metaloph; the metaloph is very simple in the two teeth from GG. However, the GG specimens are probably M^3 and may be simpler than corresponding premolars. In size of the teeth the GG specimens would fit the premolars from Push Creek, although the latter seem lower crowned even disregarding differences in wear. The latter are similar to the type of *"Anchippus" texanus* in the well developed anterior cingulum and the late connection of the protoloph to the ectoloph. They differ from the type in plications of the metaloph; in *"Anchippus" texanus* there is only one plication, the crochet.

Subfamily EQUINAE Steinmann and Doderlein, 1890

Genus *Merychippus* Leidy, 1857

Genotype: *Merychippus insignis* Leidy, 1857

Merychippus gunteri Simpson, 1930

Tables 11, 29; Fig. 4

Type. R upper premolar or molar, Florida Geological Survey V-4114, from Midway, Gadsden Co., Florida.

Occurrence. "Older" B fauna, Middle Hemingfordian of Texas Gulf Coastal Plain and Midway fauna of Florida, "younger" B and Cold Spring faunas, Lower to Middle Barstovian of Texas Gulf Coastal Plain.

Material. TMM 31057, Site 1, Barringer Farm, Moscow, Polk County: Nos. 1AB, 132 R and L upper P or M, 44 R P^2, 67 L D^2, 32, 10 2R upper D, no number P$_2$, 82, 130, 178, 129, 103 2L and 3R M$_3$, 1, 127 2L lower P, 25 R lower M, L lower D, 46, 180 2 phalanx I, 113 astragalus, 21 calcaneum, 46, 64, 203 3 phalanx II, Midwestern University No. 1473, no number L and R upper P or M, 1555 R P^2, 1554 R upper D, 1557 (4 mi. E of Moscow, Polk County) phalanx II; TMM 40081, GC & SF Railway milepost 128c N of Brenham: No. 2 R P^2; TMM 31162, Gravel Pit 15.5 mi. E of Brenham, Washington County: No. 1 R lower M; TMM 31190, Site 1, Point Blank, San Jacinto County: Nos. 15 L P$_2$, 82 L P^2, 24 R M^3; TMM 30904, 1 mi. E of George West, Live Oak County: No. 1 L lower P; TMM 40070, Sommer's Pit, Washington County: No. 27 R M$_3$; TMM 40622, Belt's Creek, Tyler County: No. 16 L lower M; TMM 40393, Quarry 1, Gonzales County: No. 15 L P$_2$, R lower M, 12 R upper P or M; TMM 40290, 2.1 mi. E of Navasota, Grimes County: Nos. 35 L ramus with P$_2$-M$_2$, 15, 28, 42 2L and 2R M$_3$, 16 R P^2, 11 phalanx I; referred TMM 31242, Site 4, San Jacinto County: No. 23, 76 2 phalanx I; TAM 2721, Loc 42, W of Hwy, Burkeville: L and R M^3, L upper P, 2L and 2R lower M, 2R and 2L lower P, R P$_2$, L M$_3$; TAM 2718, Loc 43, E of Hwy, Burkeville: L upper P, astragalus, phalanx II; TAM 2888, Burkeville, Newton County: L lower P and M (all Burkeville); TMM 31191, Site 2, San Jacinto County: No. 17 R lower P; TMM 40138, Noble Farm: Nos. 2 R P^2, 1 L M_3, TAM 2543 A L and R upper M, 2R upper P, TAM 2734, R lower M; TMM 31219, Site 3, San Jacinto County: Nos. 172, 138, 30, 52 2R and 2L lower M, 148 R lower P, 28 L upper P or M, 158F, 107 L and R upper M; TMM 31200, Site 3, 0.5 mi. NE of Site 2, Polk County: Nos. 4 L upper M, 13 R lower M; TMM 31273, 4.3 mi. N of Shiner, Lavaca County: No. 1 L upper M; TMM 31085, Brenham, Washington County: No. 5 L lower M; TMM 40122, Rd. cut 1.5 mi. E of Brenham, Washington County: No. 1 2R lower M; TAM 2540, Cold Spring: R M_3, 2539 L upper P; TAM 2570, Loc 40, Diamond Mtn., Montgomery County: L lower M (all Cold Spring).

Diagnosis. Simpson (1930, p. 165, in Quinn, 1955, p. 13): Molars subhypsodont, about as in *M. primus.* Upper cheek teeth relatively short and broad, with strong external ridges. Protocone relatively small, almost circular, with spur, and united to protoconule near apex. Pli caballin simple but normally present. One or two well defined folds on each side of the metaloph. Metastylid feebly separated on lower P_2, strongly distinct on other lower cheek teeth. Heel of M_3 small and simple, elongate.

Description. This is the most common horse in B, and is the dominating or sole species at the Barringer Farm and Point Blank sites, but in most local samples it occurs together with the more advanced *M.* sp. and *M. vetus.* In the Summer's Pit sample, which may be Lower CS (Quinn, 1955, p. 15), *M. gunteri* is sparingly represented together with *M.* sp., *M. vetus,* and *Calippus francisi.* Some low crowned teeth in the CS may belong to this species. Quinn (1955) gave a detailed description of the morphology of the teeth known to him; some variation in the tooth pattern can be commented on.

Typical and primitive features of the teeth are the ribbing of the paracone and metacone, especially pronounced at the base of the crown, the traces of a lingual cingulum, the expansion of the crown toward the top of the lower cheek teeth, and the slight height of the crown.

The protocone varies in length (table 22); in beginning of wear there is a strong spur, but the protocone does not connect to the protoconule until the tooth is worn down to about half the original height, i.e., at a mesostylar height of approximately 1.00. In the CS is a slightly worn tooth (TMM 31200-4), 1.97 high, with the protocone already connected (Quinn, 1955, plate 1:11). In some cases the protocone remains disconnected to the base of the tooth.

The hypoconal groove is well developed in beginning of wear, sometimes almost closed by a pli dihypostyle reaching lingually from the hypostyle. The hypostyle forms a hypostylar fossette opening into the postfossette. In a few specimens I have observed a hypoconal lake, which forms at the closure of the hypoconal groove; the highest tooth with a phypconal lake is 1.50. Usually the groove gradually obliterates at a mesostylar height of approximately 1.00.

In early wear the narrow and slightly sickle-shaped hypocone may be isolated from the metaloph.

The plication frequency is medium (table 22). There is almost always a pli

TABLE 11.–STATISTICS OF THE TEETH,
MERYCHIPPUS GUNTERI, B and CS

“Older” B Variate	N	M	σ	V	OR
P^3-M^2 length	6	1.54±.031	0.075	4.87	1.44- 1.64
Br.	4	2.03±.055	0.111	5.47	1.91- 2.18
P_3-P_4 length	10	1.56±.029	0.091	5.83	1.38- 1.67
Ant. br.	10	1.22±.019	0.060	4.91	1.15- 1.39
Post. br.	8	1.27±.019	0.053	4.17	1.22- 1.39
M_1-M_2 length	9	1.48±.016	0.049	3.31	1.40- 1.57
Ant. br.	7	1.18±.033	0.089	7.54	1.06- 1.30
Post. br.	6	1.15±.042	0.102	8.87	0.96- 1.18
“Younger” B and CS					
P^3-M^2 length	11	1.49±.041	0.135	9.06	1.28- 1.70
Br.	9	1.85±.051	0.154	8.32	1.68- 2.11
P_3-P_4 length	2	1.48			1.45, 1.50
Ant. br.	2	1.03			1.01, 1.04
Post. br.	2	1.13			1.09, 1.17
M_1-M_2 length	10	1.39±.032	0.101	7.27	1.25- 1.55
Ant. br.	8	1.01±.034	0.095	9.41	0.90- 1.19
Post. br.	9	0.94±.032	0.095	10.11	0.85- 1.13

caballin, occasionally forked and usually retained even in much-worn teeth.

The lower cheek teeth often have a labial cingulum, sometimes with a small protostylid. In P_2 the metaconid-metastylid column occasionally remains simple, a character which also occurs in more advanced horses. In a R and L tooth series of one individual (TAM 2727) all teeth, except M_3, are worn and all the worn teeth show a marked entoconid spur situated labially from the lingually directed entoconid, and almost touching a long pli hypoconid. In P_4 there is also a very faint posterior plication in the metaflexid. These teeth have a rounded, U-formed protoconid and hypoconid, and the parastylid in P_3-M_2 is strong at the base but fades out toward the top of the teeth.

Milk teeth. The milk teeth of *M. gunteri* differ from those of *Parahippus leonensis* in slightly larger size, less ribbing of the paracone and metacone, and in the stronger protoconal spur. Simpson (1932) described milk teeth of *M. gunteri* as lacking cement, but in the B sample the teeth which probably belong to *M. gunteri* either lack or have a cement coating, i.e., TMM 31057-10. In two milk teeth from Site 1 (TMM 31057-67 and -32) the paracone and metacone are ribbed, and the protoloph is disconnected from the ectoloph. The protocone is broadly connected in D^2; in D^3 and D^4 it is in contact with the protoconule through an anterolabial spur. In both specimens the metaloph is plicated and the crochet well developed. The hypoloph is simpler than in *P. leonensis.* The hypostylar fossette is open in D^2, and the hypostyle reaches far lingually, bordering the hypoconal groove posteriorly. There are traces of a lingual cingulum, especially anterior and posterior of the protocone.

Teeth of *M. gunteri* in the CS are smaller than in B, and the lowers especially resemble teeth of *P. leonensis.* A small sample from Town Bluff (SMU collection) comprises material of a merychippine, morphologically similar to *M. gunteri,* but larger. The CS and Town Bluff forms may be temporal and local representatives of this primitive horse; the differences between the means of "typical" Burkeville *M. gunteri* and the forms from CS and Town Bluff are not, or only erratically significant. The teeth of *M. gunteri* in the B fauna are much the same size as the ones from the type locality in Florida; the crown height may be somewhat greater in the Texas sample.

Limb bones. The limb bones from B cannot with certainty be referred to species, since in some local samples two or three forms, closely similar in size, are represented. The postcranial material from the type locality Midway, Gadsden County, Florida, is too incomplete to be conclusive as to the size of the limbs of *M. gunteri,* but the few measurements fall generally inside the range of the corresponding measurements from B.

The five complete metapodials are longer and broader than the specimens from GG, but have the same proportions. Three are from locality 4 where *M. vetus* is the most common species represented by teeth; one is from "4 mi. E of Navasota" and one from "Navasota, A&M 1933," neither associated with cranial material. A facet for the mesocuneiform is lacking and on the distal articular surface the sagittal keel is faint.

In the advanced fossil Equidae there is a trend to increase the length of the proximal medial phalanx while breadth remains unchanged (Sondaar, 1968). Thus, while in the GG sample the phalanges are rather broad and short; in B they are noticeably longer but only little broader. One observation from Midway falls in between the samples from GG and B in proportions. There is little change in the morphology of the volar ligamental scars compared to *Parahippus* from GG. The V-scar of the cruciate is very short, with the limbs of the V connected distally, and the central ligamental scar is long and forms a continuation of the distal point of the V-scar, instead of occupying a slight groove between the disconnected limbs of the V as is usually the case in phalanges from GG.

The tendency to enhance length while breadth changes little is not pronounced in the second medial phalanx. Some specimens, mainly from Point Blank and Barringer Farm, where *M. gunteri* appears to be the only species (although a small astragalus, TMM 31057-39, from Point Blank may indicate the presence there of a small equid the size of *P. leonensis* or *Calippus francisi),* are larger than the GG specimens, but otherwise of the same proportions. In this category fall also two observations from Midway. Other specimens from B seem proportionally slightly longer. However, on the basis of proportions and ligamental scars it is not possible to separate the phalanges of *M. gunteri* and *M. vetus,* considering the sometimes pronounced differences in proportions between anterior and posterior phalanges in one species.

Discussion. Compared to teeth of *P. leonensis,* teeth of *M. gunteri* are only slightly larger, but considerably higher crowned (table 23). While in

P. leonensis the crochet only seldom connects to the protoloph before the tooth is much worn; in *M. gunteri* the crochet is connected already in early wear, except in P^2 in which the connection varies. One very worn premolar (TAM 2543A) from Noble Farm shows no trace of a crochet. Except in P^2, I have not observed a single case of the metaloph not connecting to the ectoloph in *M. gunteri;* in *P. leonensis* also it is rarely disconnected in other permanent teeth than in P^2. The truncate shape and great transversal breadth of the teeth of *M. gunteri* are features in common with *P. leonensis.*

Simpson (1932) thought that *M. gunteri* may have evolved from *P. leonensis,* an opinion with which Stirton (1940), White (1942), Bader (1956), and Downs (1956) concurred. Some tooth specimens of *P. leonensis* in the ThF sample have been considered advanced enough to belong to *M. gunteri* (White, 1942). With Bader (1956) I do not think that *M. gunteri* occurs in the ThF fauna. The few specimens of *P. leonensis* with the crochet precociously connected to the protoconule do nor form a population genetically isolated from the "typical" *P. leonensis* population without a connected crochet, they only form the extremes in a continuous range of variants of this character. Specimens completely lacking a crochet are about as rare as teeth with an early connected crochet. In between these extremes is the whole range of teeth in which the crochet is developed but never connects or connects very late, and teeth in which the crochet connects at varying stages of wear.

Merychippus gunteri belongs in a group of relatively brachyodont merychippines, which could be related to each other. These are, besides *M. gunteri, M. primus, M. tehachapiensis, M. carrizoensis,* and *M. brevidontus.*

Merychippus carrizoensis from the Caliente Mountains differs from *M. gunteri* in constantly early connection of the protocone to the protoconule, and early obliteration of the hypoconal groove. The plications of the fossette borders are complicated in beginning of wear, but soon obliterated (Dougherty, 1940). In the lower teeth the metaconid and metastylid are not as well developed or as well separated as in *M. gunteri.* The height of the teeth reaches 1.60-2.30 (Dougherty, 1940).

Merychippus tehachapiensis from Phillips Ranch shows early connection of the protocone to the protoconule, but before uniting, the protocone has a strong spur.

In *M. primus* of the Sheep Creek beds of Nebraska the protocone also unites early, but there is a stage with a disconnected protocone with a strong spur. There is a well developed hypostylar fossette opening into the postfossette. The height of the unworn or little-worn upper teeth is 1.60-2.49, mean 2.25 ± .04.

Merychippus brevidontus from the Mascall is somewhat younger than the species mentioned above, but no more advanced. Bode (1934) gave the height of the unworn teeth as 1.87-2.34, with a mean of 2.05, which is about the height of the teeth of *M. carrizoensis. Merychippus brevidontus* is very similar to *M. gunteri* in short protocone with pronounced spur in beginning of wear, open or closed hypostylar fossette, pronounced pli hypoconid and entoconid spur of the lower premolars, and marked lingual cingulum in the uppers and labial cingulum with a protostylid in the lowers.

Merychippus brevidontus is larger than *M. gunteri* from B and CS.

Merychippus vetus (Quinn), 1955
Tables 12, 30; Figs. 4, 5A, 5B

Protohippus vetus Quinn, 1955

Type. R and L maxilla with P^3-M^3 and P^2-M^3, TMM 31242-71, from Site 4, San Jacinto County, Texas (Quinn, 1955, plate 1, figs. 14, 15).

Occurrence. "Younger" B fauna, Lower Barstovian of Texas Gulf Coastal Plain.

Material. TMM 31162, gravel pit 15.5 mi. E of Brenham, Washington County: Nos. 2 R lower P, 3 upper P; TMM 31242, Site 4, San Jacinto County: Nos. 82, 103, 2L lower M, 84 R and L M_3, R P_2, R D_2-D_4, 52, 61 R and L upper M, R upper P, L M_3, 14, 60 L and R upper P or M, 72 R P^2, 71 R and L P^2-M^3 (type *Protohippus vetus*), 100 R and L D^2-D^4, 5 L ramus with P_2-M_3, 81 R P_4-M_1, 28 proximal radius, 50, 80 2MC III proximal, 109 distal tibia, 6, 86, 3 MT III, 22 proximal MT III, 31, 50, 67, 74, 105 6 distal metapodials, 24, 45, 2 astragali, 4, 59, 63, 65, 91, 95 6 calcanea, 32, 50, 66, 76, 95, 98 9 phalanx I, 23, 3, 32, 50, 66, 68, 76, 10 phalanx II; TMM 31243, Site 5, San Jacinto County: No. 3 L upper P or M, R upper P; TMM 40070, Sand pit, Summer's Ranch, Washington County: Nos. 3, 17 2R upper P, 25 L upper P or M, 4, 24 R and L upper M, 12 R and L lower M, 1 R lower D; TMM

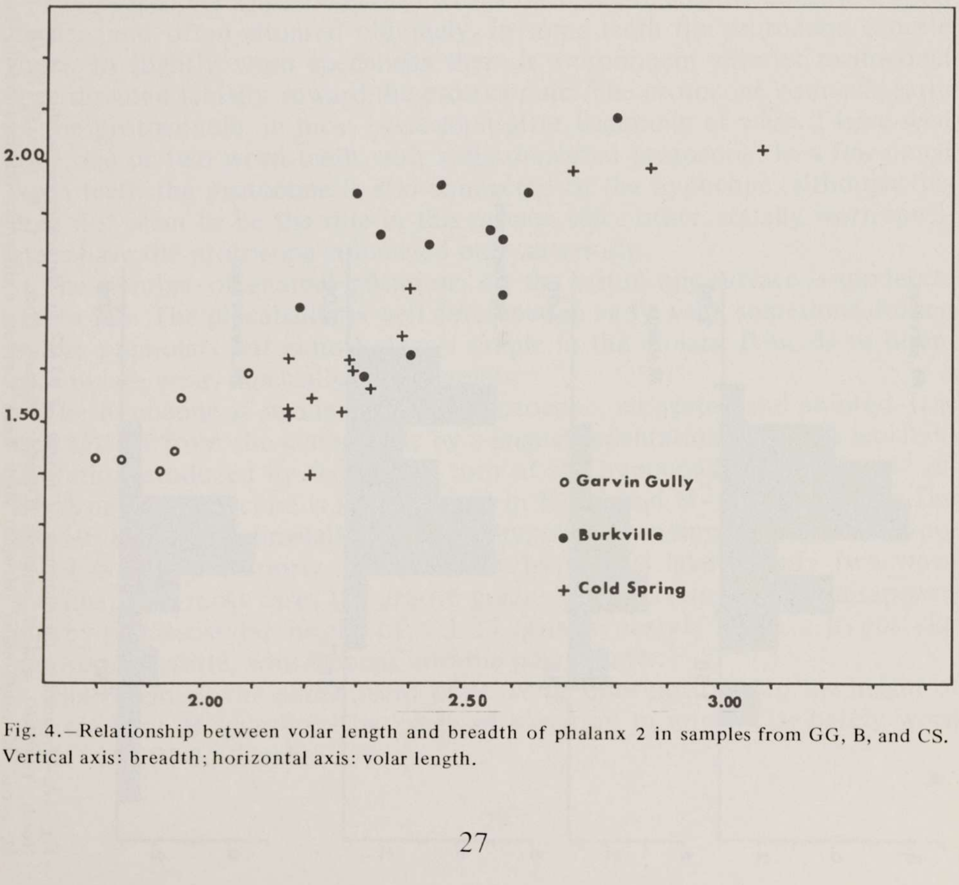

Fig. 4.—Relationship between volar length and breadth of phalanx 2 in samples from GG, B, and CS. Vertical axis: breadth; horizontal axis: volar length.

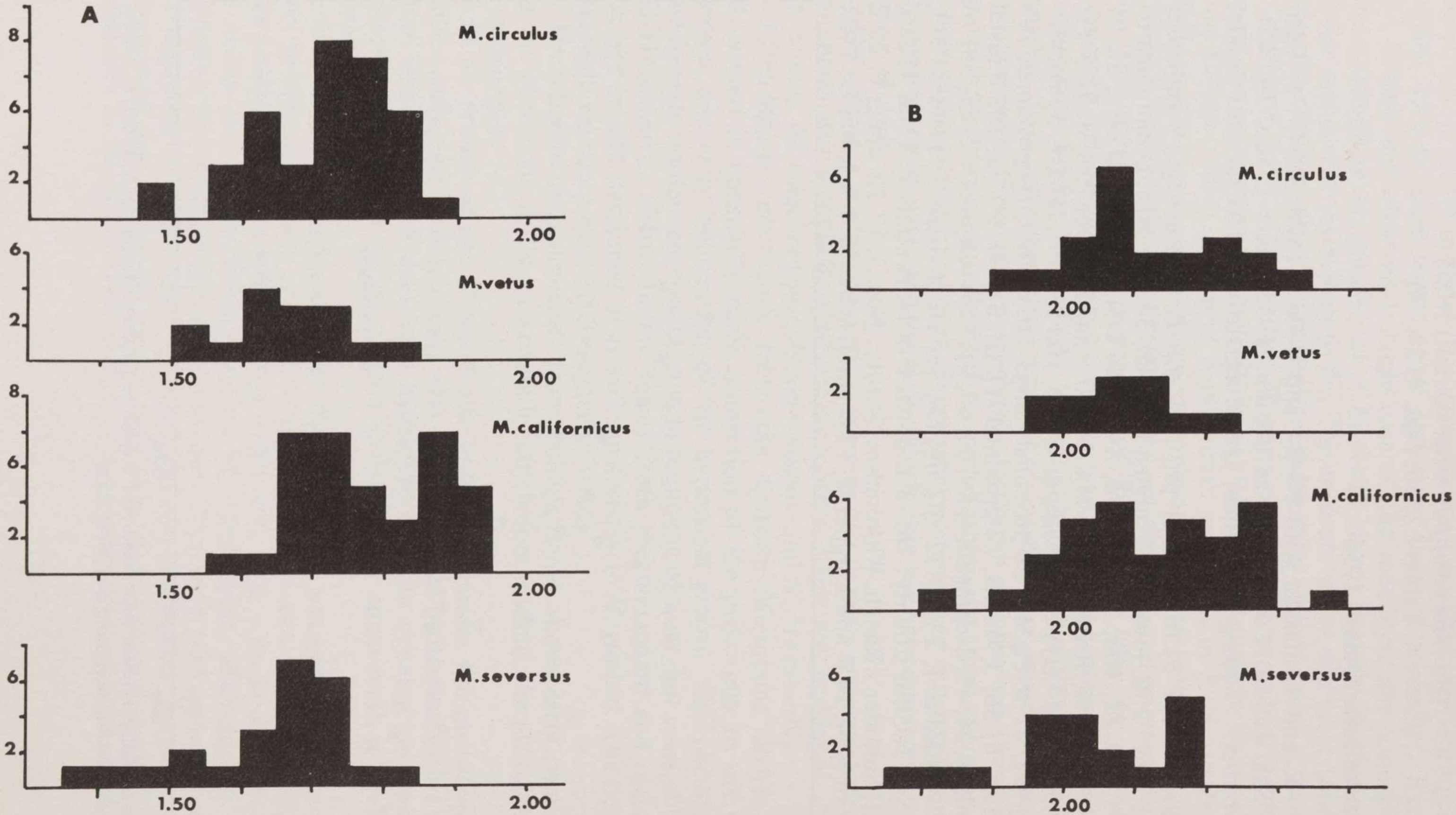

Fig. 5A.—Frequency distributions of length of P^3-M^2 in *Merychippus circulus, M. vetus, M. californicus* (Nevada: High Rock Canyon; California: Coalinga North, Temblor), and *M. seversus* (Oregon: Mascall, Locs. –, 5, 8, 14, 15, 17). 5B.—Frequency distributions of breadth of P^3-M^2 in *Merychippus circulus, M. vetus, M. californicus* (Nevada: High Rock Canyon; California: Coalinga North, Temblor), and *M. seversus* (Oregon, Mascall, Locs. –, 5, 8, 14, 15, 17).

40141, Red Hill: No. 3 R lower M; TMM 40622, Belt's Creek, Tyler County: Nos. 18, 19 R lower M, 17, 20, 22 3L lower P, 24 L P^2-P^3, 21 P^2, 15 L M$_3$, 14 L D$_2$, 11 phalanx II, 7 2 distal metapodials, 10 astragalus; TMM 40623, Push Creek, Tyler County: Nos. 8 2R lower M, L lower M, L M$_3$, 15 5 L and R uppers; TAM 2726, Burkeville, W side Hwy, L lower P; TAM no number, Navasota: MT III; TMM 40453, Site 4, San Jacinto County: No. 1 MT III; TMM 31244, Site 6, San Jacinto County: No. 5 astragalus.

Diagnosis. Quinn (1955, p. 17, revised): Hypsodont. Ectoloph flattened with styles and ribs strongly developed; protocone long-oval and disconnected at the summit of the crowns, seldom lower down. Pli caballin on all cheek teeth in early wear, lost with wear on molars but not on premolars, bifurcate on sone premolars. Hypostylar fossette present on some molars. Lower cheek teeth with rounded protoconid and hypoconid; parastylid variable.

Description. Together with the low crowned *Merychippus gunteri* there occurs in B a larger, more advanced species of this genus. Quinn (1955) described part of the material as a new species, *vetus,* of the genus *Protohippus.* This form was based on a R and L upper tooth row (TMM 31242-71) of one individual, and a referred isolated lower molar (TMM 31242-103). Although M^3 is barely coming into wear the protocone of M^1 is already connected to the protoconule. Some additional material referable to *M. vetus* places it, mainly on the basis of the rather long, partly disconnected protocone, in a group of merychippine horses to which also belong *M. seversus* (including *M. isonesus* (Downs, 1956), *M. californicus, M. insignis,* and *M. sejunctus.*

The protocone is narrowly oval with a flattened or slightly concave lingual border, and often situated obliquely. In some teeth the protocone is quite short. In slightly worn specimens there is a prominent anterior protoconal spur directed labially toward the protoconule. The protocone connects early to the protoconule, in most cases soon after beginning of wear. I have seen only one or two worn teeth with a disconnected protocone. In a few much worn teeth the protocone is also connected to the hypocone, although this does not seem to be the rule in this species, since other, equally worn specimens have the protocone connected only anteriorly.

The number of enamel plications on the triturating surface is moderate (table 22). The pli caballin is well developed in early wear, sometimes forked in the premolars but almost always simple in the molars. It tends to disappear in late wear, especially in the molars.

The hypocone is smaller than the protocone, elongated and pointed. It is well set off from the metaconule by a lingual indentation, and by a labial indentation produced by the lingual turn of the hypoconal groove. In M^3 of the type the hypocone is isolated, and in P^3-P^4 and M^2 it is nearly so. The hypostyle extends lingually in a pli dihypostyle tending to close the hypoconal groove posteriorly. I observed a hypoconal lake in only two worn specimens; in most cases the groove gradually obliterates, usually disappearing by a mesostylar height of ± 1.25. The hypostyle forms a hypostylar groove or fossette, which opens into the postfossette.

The height of the cheek teeth of *M. vetus* does not overlap the height of the teeth of *M. gunteri.* The range of variation in unworn or barely worn P^3-M^2 is 3.01-3.50 (table 23).

TABLE 12.–STATISTICS OF THE TEETH,
MERYCHIPPUS VETUS, B

Variate	N	M	σ	V	OR
P^3-M^2 length	15	1.66±.022	0.086	5.15	1.50- 1.84
Br.	12	2.08±.022	0.076	3.67	1.95- 1.24
P_3-P_4 length	3	1.68			1.60- 1.73
Ant. br.	3	1.28			1.16- 1.35
Post. br.	3	1.27			1.10- 1.40
M_1-M_2 length	13	1.65±.020	0.071	4.30	1.50- 1.79
Ant. br.	12	1.16±.033	0.115	9.91	0.95- 1.39
Post. br.	13	1.02±.032	0.117	11.42	0.85- 1.29

Quinn (1955) described one referred lower molar (TMM 31242-103) and observed the difference in morphology between this specimen and teeth of *"Pliohippus" circulus* of CS, a difference which is mainly due to differences in the stage of wear of the teeth of each taxon. In the described molar of *M. vetus* the parastylid is only a low ridge sloping across the anterior side of the tooth; in most teeth of this species the parastylid is a well developed structure.

The pli hypoconid and entoconid spur are prominent, as Quinn stressed. In one premolar the entoconid spur is trifurcate. The height of P_3-M_2 is 2.50-3.30.

Milk teeth. Quinn (1955, p. 64) commented on the similarity of the milk teeth of TMM 31242-84 to the type of *M. insignis.* The deciduous teeth in the B sample do resemble those of *M. insignis* in thin cement coating and in orientation and form of the protocone and hypocone. The teeth of *M. vetus* are larger and better cemented than those of *M. gunteri,* but similar in having a protocone with a strong anterolabial spur and constricted hypocone, and in the structure of the hypostyle with an open or closed fossette, and pli dihypostyle closing the hypoconal groove posteriorly.

In the lower milk teeth the metaconid and metastylid are long and oval in early wear, in late wear more rounded. The loops are of equal size or the metaconid is slightly larger, and are separated by a deep lingual V-groove persistent to the base. In later stages of wear the flexids obliterate. The paralophid, which points lingually in early wear, becomes broad and flattened or even slightly bifurcated. The hypoconulid is long and well constricted from the entoconid, which has an anteriorly directed spur. The cingulum is well developed: anteriorly there is a transversely long parastylid separated at the top from the paralophid, a lingual protostylid, and a low posterior hypostylid. A cingulum can also be traced labially around the protoconid.

Discussion. Merychippus vetus represents a stage of evolution comparable to *M. seversus* from the Mascall and *M. californicus* from N. Coalinga, and is also morphologically similar to thses species. It differs from *M. seversus* in slightly larger size of the teeth, and possibly slightly greater hypsodonty. Also, the protocone and hypocone are longer and narrower, and the pli caballin weaker in worn teeth of *M. vetus. Merychippus vetus* is similar to *M. seversus* in well developed pli dihypostyle.

Merychippus californicus is only little larger than *M. vetus*, but definitely more hypsodont. It also differs in a tendency for the prefossette, especially of the premolars, to remain open into the postprotoconal valley because of a failure of the crochet to close early in wear. This is not evident in *M. vetus*, except in P^2. In both *M. seversus* and *M. californicus* there is a tendency for the postfossette to open into a hypostylar fossette; this also occurs in *M. vetus. Merychippus vetus* differs from both species in the early connection of the protocone to the protoconule, whereas in *M. seversus* and *M. californicus* the protocone remains disconnected until the tooth is well worn. Some specimens of *M. seversus* (Downs, 1956, fig. 28) have a connected protocone although the teeth are not much worn, but in this species early connection does not appear to be the rule, as in the case in *M. vetus*.

I compared data in Downs (1956) on limb bones referred to *M. seversus*, and data on material from the Mascall which I measured myself, with data from B. The metapodials in the B sample are longer and narrower than metapodials referred to *M. seversus*. The proportions of tibia and radius are unknown in the B sample, but distal breadth of these bones is the same in the samples. Astragalus is slightly broader distally, and higher in the Mascall sample, but calcaneum and the first medial phalanx have approximately the same size and proportions. The postcranial material from Barstow has the same proportions as in the B sample, but most measurements are larger.

Merychippus insignis from the Snake Creek beds of Nebraska, recently considered a possible descendant of *M. californicus* (Downs, 1956), is also larger and more hypsodont than *M. vetus*, and has a protocone with spur which remains disconnected until the tooth is quite worn.

In *M. sejunctus* from the Pawnee Creek beds of Colorado the protocone connects early to the protoconule. *Merychippus sejunctus* further resembles *M. vetus* in development of the hypostyle, which in the latter species extends lingually in a pli dihypostyle partly closing off the hypoconal groove, and in the tendency for the hypoconal groove and the pli caballin, both of which are well developed in early wear, to obliterate in later stages of wear. The Pawnee Creek merychippines are not well known due to splitting and possible mixing of material from different levels. *Merychippus sejunctus* differs from most *M. (Protohippus)* in the long, narrow protocone and hypocone, relatively high plication count, and tendency for the fossettes to remain transversely narrow. In *M. perditus* and *Pliohippus simus* the protocone is long and narrow, but the fossettes are very open and the plication frequency quickly decreases with wear. In other species of *M. (Protohippus)* the protocone is short, rounded, and soon broadly connected as a part of the protoloph. The hypoconal groove quickly obliterates, the plications are few and disappear completely as the fossettes become very open and transversely broad.

Merychippus circulus (Quinn), 1955

Tables 13, 31; Figs. 4, 5A, 5B

Pliohippus circulus Quinn, 1955
Eoequus wilsoni Quinn, 1955

Type. R lower tooth series with P_4-M_3, TMM 31191-10, from Site 2, San Jacinto County, Texas (Quinn, 1955, plate 3, fig. 8).

Occurrence. Cold Spring fauna, Middle Barstovian of Texas Gulf Coastal Plain.

Material. TMM 31184, Site 2, Polk County: No. 30 skull (type *Eoequus wilsoni* Quinn), 37 R and L jaw belonging to skull; TMM 31183, Site 2, Polk Co. Nos. 6, 51 2 radii, 85 proximal MC III, 38 distal metapodial, 28 calcaneum, 83 phalanx I; TMM 40418, Cold Spring, Washington Co.: No. 3 2R and L upper P, 5 astragalus, TAM 2539 R and L uppers, TAM 2540 R lower D; TMM 40138, Noble Farm: R lower P, TAM 2533 R and L uppers, TAM 2734 R and L lowers, TAM 2543 and 2543A 2L upper P; TMM 40196, Trinity River, Pit 1, San Jacinto County: L upper M, phalanx I; TMM 31200, Site 3, Polk County: Nos. 5, 10 2 astragali; TMM 31219, Site 3, San Jacinto County: Nos. 43 R juvenile ramus with D_2-D_4, 204, 277 2R ramii with P_4-M_3, 203 R and L juvenile ramii with D_2-D_4, 164, 43, 106 3R lower M, 159 R lower M, L M_3, L P_3-M_2, 147, 138, 32 3L lower M, L and R M_3, 172, 148 2R lower P, 147 L P_2, 280 R D_2, 82 L M_3, R P_2, 165 R and L D^2-D^4, M^1-M^2, 230 R and L D^2-D^4, M^1-M^2, 160 R upper P or M, 165E, 253 2R upper P, 96, 146, 158 B 3L upper P, 118 R and L upper P, 61 L P^2, 107 R and L P^2, 4 L upper M, 5 L M^3, 205 MT III, 124 astragalus, 192 calcaneum, 190, 83 2 phalanx I, 20, 153 3 phalanx II; TMM 31244, Site 6, San Jacinto County: No. 1 L M_3; TMM 31272, Chapel Hill, Washington County: No. 33 R and L M_3, 8 L M^3; TMM 31085 first outcrop E of Union station, Brenham, Washington County: No. 1 R M^3; TMM 880, South Bluff of South Harvey's Creek, Colorado County: No. 1 R upper and lower M^3_3; TMM 31191, Site 2, San Jacinto County: No. 10 R P_4-M_3 (type *Pliohippus circulus* Quinn); TAM Barry Farm, Grimes County: R lower P; TAM 2570, Loc. 40, Diamond Mountain, Montgomery County: L upper M; TAM no number, ?Noble Farm: MT III, phalanx I; TAM 2876, Mound Creek, Montgomery County: MC III proximal fragment, 2 astragali.

Diagnosis. Quinn (1955, pp. 23, 54, revised): Hypsodont. Teeth moderately curved; protocone elongate, slightly heeled and grooved in early wear; disconnected at summit of crown, but with long spur. Plication frequency moderate. Lower teeth with protoconid and hypoconid slightly flattened in early, rounded in later wear; metaconid and metastylid wide, flaring in early, rounded in late wear. Incipient pli caballinid; parastylid variable.

Description. Merychippus vetus of B probably gave rise to a similar large and hypsodont merychippine in CS. The material of this horse was described by Quinn as two species, but it is impossible to sort out two taxa in the sample of isolated teeth, and when Quinn's descriptions of the features of the types and referred teeth are compared, they are identical or differ due to differences in the stage of wear of the specimens described. *Merychippus circulus* has page priority. This species is morphologically similar to *M. vetus*

TABLE 13.—STATISTICS OF THE TEETH,
MERYCHIPPUS CIRCULUS, CS

Variate	N	M	σ	V	OR
P^3-M^2 length	31	1.70 ±.016	0.087	5.12	1.45- 1.86
Br.	22	2.09 ±.022	0.102	4.89	1.93- 2.33
P_3-P_4 length	8	1.70 ±.041	0.116	6.84	1.55- 1.79
Ant. br.	7	1.20 ±.040	0.107	8.95	1.11- 1.45
Post. br.	7	1.28 ±.049	0.129	10.10	1.21- 1.43
M_1-M_2 length	19	1.70 ±.025	0.110	6.49	1.42- 1.85
Ant. br.	18	1.16 ±.021	0.068	5.89	1.05- 1.43
Post. br.	17	1.06 ±.031	0.097	9.18	0.94- 1.27

but more hypsodont (table 23).

As in *M. vetus* the protocone is long (table 22), lingually flattened, and has a prominent anterolabial spur, which connects to the protoconule in early wear. The connection remains narrow throughout. In a few cases the protocone also connects to the hypocone. This is more common and is established earlier in the molars than in the premolars; only much worn premolars may have the protocone connected to the hypocone. Quinn described the protocones in *Pliohippus circulus* and *Eoquus wilsoni* as similar, except that he assumed the protocone-hypocone connection to characterize *M. circulus.* I have noticed this feature in *M. vetus,* and it occurs occasionally in worn teeth of most merychippines.

Quinn placed *circulus* in the genus *Pliohippus* on the basis of the protocone-hypocone connection and the reduced styles of the referred upper molars (TMM 31219-165A, D). This specimen is a juvenile with molars just erupting; in describing the sectioned M^2 Quinn noted the more strongly developed styles at the level of sectioning in that specimen than in M^1. The strength of the styles varies with location of the tooth in the jaw, premolars have stronger styles than molars, with the stage of wear, becoming stronger toward the base, and individually. In M^1 of the types of *P. circulus* and *E. wilsoni* the styles are equally strong.

The plication count is little different from that in *M. vetus* (table 22), and Quinn gave identical descriptions of the plications of the fossettes in *P. circulus* and *E. wilsoni.* Especially in the premolars, the fossettes tend to remain transversely narrow, and the main plications are visible even in much worn teeth. In the molars the fossettes may become wide and open, and the fossette borders lose their plications when the tooth wears down. Worn molars in their simplified pattern resemble those of *M. (Protohippus).*

The hypocone is long and narrow in early wear, and well marked off from the metaconule by a lingual indentation and by the hypoconal groove, which remains open until late wear. I have not observed a single case of the groove enclosing a lake, which sometimes is the case in *M. vetus;* rather, it gradually obliterates and disappears at a mesostylar height of + 1.00. Quinn observed a hypostylar fossette in M^2 of the type of *E. wilsoni;* the referred M^1 of *P. circulus* does not have a hypostylar fossette, which also is absent in M^1 of *E.*

wilsoni. The expression of this character is clearly dependent on the stage of wear of the tooth. As in *M. vetus* there is a strong tendency for the hypostyle to reach lingually in a pli dihypostyle, posteriorly closing off the hypoconal groove; sometimes additional plications from the hypostyle reach into the groove.

The morphology of the lower teeth is advanced, especially in early wear. The little worn premolars in the type of *E. wilsoni* have wide, flaring metaconid-metastylid columns and incipient pli caballinids. The lower molars in early wear may be confused with molars of *Hipparion* with their sometimes long metaconid and metastylid. This is the case with the specimen (TMM 31219-43), which Quinn (p. 57) referred to *Hipparion.* In worn teeth the columns soon become shorter and more rounded, and the flexids tend to obliterate.

The protoconid and hypoconid are slightly flattened in the type premolars of *E. wilsoni,* rounded in *P. circulus;* the conids of the molars are rounded in both type specimens. The difference in the premolars seems to be due to differences in wear.

The parastylid varies in height and strength; in the type of *E. wilsoni* it is well developed, but in the type of *P. circulus* it is visible only as a slight scar along the anterior side of the tooth.

Milk teeth. The milk teeth are morphologically advanced over those of *M. vetus* in being higher crowned and better cemented; the protocone and hypocone are longer and more pointed, and the lophs more complicated. The crochet tends to close already in mid-wear. As in *M. vetus* the protocone has an anterior labial spur, and the hypocone is isolated in early wear. There is a hypostylar fossette, and one or two plis dihypostyle in the hypoconal groove, which is partially closed off. The hypoconal groove remains open to the base. The lingual cingulum is well developed anterior and posterior of the protocone, sometimes forming high, partially isolated styles.

The lower milk teeth have strong cingular structures, much as in *M. vetus:* there is a transversely long, narrow parastylid, protostylid, and hypostylid, broadly rounded or bifid paralophid, and marked hypoconulid. The metaconid is long, angularly oval or rounded oval in late wear, and usually larger than the rounded metastylid. The entoconid has a well developed anterior spur; in D_2 the spur reaches a long pli hypoconid.

The skull. The skull (TMM 31183-30), which is the type of *Eoequus wilsoni* Quinn, is vertically crushed, which has caused the bone to crack, almost obliterating the sutures. The cranial foramina, even the large infraorbital foramen, are largely invisible due to filling with matrix.

The lacrimal fossa is situated close to the orbit just under the nasals. It is well marked posteriorly by a rather deep pocket, but anteriorly it merges with the surface without clearly defined limits. The fossa is ventrally filled up by the high, newly erupted permanent teeth, but appears narrowly pear-shaped with the broad end posteriorly. This is also the shape of the fossa of the juvenile specimen, TMM 31219-230, which Quinn (p. 57) thought belonged to *Hipparion.* The lacrimal fossa ends posteriorly at a level with the mesostyle of M^2, and runs forward as far as the buccal fossa; its great length is probably spurious and due to crushing of the skull. There is no trace of a masseteric fossa.

The snout is long and rather broad. The dorsal rim of the premaxilla is almost straight, and the nasal opening seems long.

Limb bones. As in the B sample the postcranial material is hard to refer to species. *Merychippus circulus* is the largest horse in the fauna, and a number of specimens may belong to this form. Two MT III are longer and broader, but proportionally similar to those tentatively identified as belonging to *M. vetus.* Some proximal medial phalanges are longer, but hardly broader than those from B, thus proportionally more slender. *Merychippus circulus* is advanced over earlier forms in that ulna is distally fused to radius.

Discussion. Merychippus circulus is very similar to *M. vetus;* Stirton (in a letter to Wilson) believed the former to be "close to a direct lineage" from the latter, and further believed that this line evolved on into *Nannippus retrusus* and *N. gratus,* i.e., species now referred to the genus *Pseudhipparion.* Webb (1969, p. 133) also believed that *M. "wilsoni"* may be close to the line to *Pseudhipparion.* I do not think that *M. circulus* is closely related to *Pseudhipparion.* The constant early connection of the protocone to the protoconule and the gradual closing of the hypoconal groove differ from the erratic mode of the protocone connecting to the protoconule and/or to the hypocone, and the frequent and early closing of a hypoconal lake in *Pseudhipparion.* There are similarities in the lacrimal fossa, which in *P. gratum* is small, oval, and situated high under the nasals, and in the lack of a massateric fossa.

The skull of *M. sphenodus* (Osborn, 1918, plate 10, fig. 2, plate 12) is similar to that in *M. circulus* in the small, rather deep lacrimal fossa situated on a level with M^1-M^2 and P^3, and lack of a masseteric fossa. The tooth pattern is also similar, except that the protocone does not connect to the protoconule until late wear.

Downs (1956) described and figured several skulls of *M. seversus.* There is variation in form and extent of the preorbital fossa, but in none is there a well developed masseteric part. *Merychippus californicus,* probably a descendant of *M. seversus* (Downs, 1961), and *M. circulus* are about the same size and equally hypsodont, but as in *M. sphenodus* and *M. seversus* the protocone in *M. californicus* remains disconnected until the tooth is well worn.

In discussing *M. vetus* I compared the teeth with those of *M. sejunctus* of the Pawnee Creek beds and noted many characters in common. The teeth of *M. circulus,* too, are similar to those of *M. sejunctus,* except that the protocone of the former is longer and more pointed. The skull of *M. sejunctus* differs in the very short nasal opening and in the very broad, rounded preorbital fossa consisting of a lacrimal and a masseteric part (Osborn, 1918, plate 20). Basal length of the skulls of *M. sejunctus* and *M. circulus* is similar, 32.5 and 33.0.

Merychippus sp. near *Hipparion*

Tables 14, 32; Fig. 4

Occurrence. "Younger" B fauna, Lower Barstovian, and CS fauna. Middle

Barstovian of the Texas Gulf Coastal Plain.

Material. B: TMM 31242, Site 4, San Jacinto Co.: No. 87 R M_3; TMM 31243, Site 5, San Jacinto Co.: No. 1 L M^1-M^3; TMM 40070, Summer's Pit, Washington Co.: Nos. 12, 17 R and L lower M, 5 L upper D, 3 L upper M, 2 R upper P or M; TMM 40674, Summer's Ranch, Texas 90 rdcut, Washington Co.: No. 4 L P^2; TMM 40622, Belt:s Creek, Tyler Co.: No. 8 R M_3; Cold Spring: TMM 31191, Site 2, San Jacinto Co.: Nos. 18 L M^3, 11, 18, 2L, R upper M, L upper P, 2 L lower M; TMM 40138, Noble Farm: Nos. 4 R lower P, TAM 2390, L M_3, L P^2, TAM 2543A, R upper P and M, L upper P or M, 2R and L M^3, TAM 2733, L upper M, L M^3, TAM 2734, 2L and 2R lower M, 2R and 6L lower P, R D_2, lower D, R P_2, TAM 2544, L upper P and M, ?TAM 2549, distal metapodial; TMM 40418, Cold Spring, Washington Co.: Nos. 3 L lower M, 4 phalanx II; TMM 40196, Trinity River, Pit 1, San Jacinto Co.: No. 28 R upper M, 1 phalanx II; TMM 31219, Site 3, J. Donahoe Farm, San Jacinto Co.: Nos. 284 L D_3-D_4, 286 R ramus with M_1-M_2, 203 L ramus with P_2-M_1, R ramus with P_3-M_3 (not the same individual), 189 L and R P^3-M^3 and snout, 224 skull, 164, 168A, 203, 162, 127, 63, 280, 31, 9, 175, 122, 106, 166 3R and 10L lower M, 172, 168B, 8, 147, 95, 175, 255, 114, 82, 4L and 6R lower P, 2, 51, 112, 158G, 139, 197B, G, 158D 8R and 1L upper M, 24, 51, 165, 158I, 146, 107, 139, 118, 197D, A, C, E, 67, 158A 7L and 8R upper P, 26, 243, 146 2R and 1L upper P or M, 147, 138, 175, 114, 106, 82, 5R and 3L M_3, 27, 81, 62, 121, 112, 146, 107, 139, 176, 197H, 143 6R and 10L M^3, 133, 146, 67, 143, 2L and 2R P^2, 112 L upper D, 145 L P^2-P^4, 152, 185 2 astragali, 90, 270 2 calcanei, 68, 140 2 phalanx I, 12, 13, 65, 71, 94, 85, 116, 130, 136, 169 13 phalanx II; TMM 31183, Site 2, Polk Co.: Nos. 75 L ramus with P_3-M_3, 23 L ramus with P_3-M_3, 11 L P^3-M^1, 90 R P^2-P^3, 95, 96 L and R lower P, 20, 39 R upper and lower M^3_3, 15 R lower D, 69, 88, 94 3 astragali; TMM 31200, Site 3, Polk Co.: Nos. 9 R juvenile ramus with D_4-M_2, 13 L lower P, 3 R lower M, 6 phalanx II; TMM 31272, 4 mi SE Chapel Hill, Hwy 290, Washington Co.: Nos. 9 R lower M, 11 R lower P, 7, 32 2L upper M, 6 L upper P or M, 31, 34 2 distal metapodials; TMM 31245, Site 1, Fayette Co.: no no. L D_2-D_4 and M^1, R D_2 and M_1, 7 distal metapodial; TMM 31085, Brenham, Washington Co.: R upper P; TMM 31244, Site 6, San Jacinto Co.: No. 1 R lower M; TAM 2539, Loc 38, Cold Spring, San Jacinto Co.: L M^2 and M^3, L and R upper M, R upper P, L upper P or M, 2R M^3, TAM 2540, L and R lower M, 4L lower P, R D_2; TAM 2570, Loc 40, Diamond Mtn., Montgomery Co.: L and 3R upper M, R upper P, L lower M, L and 3R M^3; TAM 2876, Mound Creek: astragalus, distal metapodial.

Description. Probably the most common horse in CS is a merychippine with traits resembling *Hipparion.* This species is rare in B, but is found at all CS sites together with *Calippus francisi*, *Merychippus circulus*, and *M. gunteri.*

The teeth are hypsodont (table 23). In size, hypsodonty, and morphology, this form overlaps *M. gunteri* in the same fauna, and isolated teeth may be hard to classify. Some lower teeth resemble *M. vetus* and *M. circulus* or *Calippus francisi* in morphology and proportions. The tooth crowns taper anteroposteriorly toward the base; this is more pronounced in the lowers than in the uppers, and in the relatively low-crowned specimens more than in the hypsodont ones, but the teeth are transversely narrower than the teeth

TABLE 14.–STATISTICS OF THE TEETH,
MERYCHIPPUS SP. NEAR *HIPPARION*, CS

Variate	N	M	σ	V	OR
P^3-M^2 length	53	1.54 ±.016	0.115	7.44	1.30- 1.76
Br.	39	1.88 ±.019	0.121	6.42	1.55- 2.14
P_3-P_4 length	20	1.69 ±.017	0.076	4.51	1.55- 1.86
Ant. br.	16	1.05 ±.012	0.050	4.76	0.95- 1.19
Post. br.	20	1.09 ±.012	0.055	5.08	0.96- 1.19
M_1-M_2 length	16	1.56 ±.020	0.079	5.09	1.40- 1.83
Ant. br.	16	0.99 ±.020	0.079	7.96	0.94- 1.20
Post. br.	12	0.91 ±.024	0.083	9.11	0.82- 1.10

of *M. gunteri*, *M. vetus*, and *M. circulus*.

The mesostyle is pointed at the top of both the premolars and molars, sometimes incipiently grooved in the premolars; the parastyle is pointed or broadly rounded in the molars, often bifurcate in the premolars. The styles broaden toward the base.

The upper teeth are distinguished by the protocone, which remains disconnected until the tooth is much worn; all teeth under 1.00 have a connected protocone. In a few M^3s I have observed the protocone to connect at an earlier stage of wear; this is also typical of M^3 in some populations of Eurasian *Hipparion*. Only in much-worn teeth may the protocone connect both to the protoconule and the hypocone. The protocone of the molars is hipparionine, long and lingually somewhat flattened with marked anterior and sometimes posterior spur. The protocone of the premolars is shorter, often very short and rounded, with a strong anterior spur directed toward the protoconule. The spur is pronounced in early wear, but tends to disappear in late wear, especially in the molars. The mean protoconal length of this species is less than in *Calippus francisi*, which has smaller teeth. This is due to the short protocone of the premolars in *M.* sp., while in *Calippus* the protocone is long in both premolars and molars (table 22).

The hypocone is long and narrow, of roughly the same size as the protocone, sometimes disconnected from the metaloph in early wear and with a lingual indentation persistent throughout wear. The hypoconal groove is deep and remains usually open to the base of the tooth; in a few specimens there is a hypoconal lake, which forms earliest at a mesostylar height of about 1.00. This character, too, is more common in M^3 then in the other teeth. In much-worn teeth the hypoconal groove may be obliterated, but usually it remains deep throughout wear. This species frequently has multiple plis dihypostyle, but in almost all specimens there is at least one plication formed by a lingual extension of the hypostyle.

The plication frequency is medium to quite high, the mean plication count far surpasses any other species in CS or earlier faunas (table 22). The pli caballin is often forked. The pli protoconule is also forked, or simple where the pli caballin is simple, i.e. often in molars. In worn teeth, too, the plication count remains high.

In some cases remains of a lingual cingulum are visible.

Frequently the posterior fossette opens into a hypostylar fossette, which occasionally is closed forming a small, isolated lake. There is no apparent tendency for the fossettes of the permanent teeth to remain open, i.e. for the crochet to fail to close, in this species. In P^2 the crochet often does not connect to the protoloph, and the protoloph and metaloph may not connect to the ectoloph, thus leaving the anterior fossette open in the post-protoconal valley and in contact with the posterior fossette.

In the lower premolars the metaconid-metastylid column is well developed, with a broadly V-shaped lingual groove between the loops to the base of the tooth. In beginning of wear the loops droop labially, with marked lingual turn of the flexids; with increasing wear the metastylid becomes triangular. There is a pli hypoconid and occasionally a posterior plication in the metaflexid. I have also observed a pli caballinid in some premolars. In one case the paralophid has plications directed posteriorly into the metaflexid. The groove between the labially slightly flattened protoconid and hypoconid is often deep in beginning of wear, and reaches as far lingually as the commissure between the metaconid and metastylid; in some cases the groove is shallow, and the metaconid-metastylid column balances on a narrow stalk as is usually the case in advanced horses. In some little-worn premolars the metaconid-metastylid column is completely isolated from the stalk, or either is isolated from the other which remains connected. The entoconid is oval with one or two spurs pointing toward the pli hypoconid. There is an anterior cingulum running diagonally across the anterior surface of the tooth, often forming a more or less well developed parastylid. With increased wear the metaconid merges with the paralophid, leaving an isolated metaflexid lake, and the entoflexid obliterates.

In the molars the metaconid and metastylid are separated by a shallow lingual groove and a deep labial groove. The two loops of the column are usually far apart in beginning of wear, connected by a narrow, longitudinal commissure. In early wear the loops may droop slightly, in later wear they are oval. There is a pli hypoconid and sometimes a small posterior plication in the metaflexid. There is no pli caballinid. As in the premolars the parastylid varies from a slight anterior cingulum running transversely up the anterior side of the tooth to a well developed, loop-like stylid. The entoconid is oval, pointed, and reaches out toward the pli hypoconid. There is a well developed hypoconulid set off from the entoconid in both molars and premolars; in M3 the hypoconulid is very long.

The proportions of the teeth of this species place it among horses with relatively narrow tooth crowns; the length-breadth proportions of the crowns are similar to those of *Calippus francisi. Merychippus gunteri* and *M. circulus* have broader teeth. In *M.* sp. and *C. francisi* the teeth are also less curved than in *M. circulus* and *M. gunteri.*

Milk teeth. A few juvenile jaw fragments and isolated lowers are referred to this species because the teeth are somewhat too small for *M. circulus* and too large for *C. francisi.* The pattern of the lowers is simple: the metaconid is slightly angularly oval, and larger than the rounded-oval metastylid. In early wear the stylids droop slightly, with the tip of the metaconid curved back. The entoconid is oval with a pointed, anterolabially directed tip, and well constricted from the hypoconulid. The protoconid and hypoconid are rounded. In early wear the hypoconid may be isolated from the metaconid-metastylid column. The cingulum is weaker than in *M. vetus* and *M. circulus;* the parastylid and usually the protostylid are developed, but the hypostylid is absent.

The skull. From Site 3 there are a partial skull (TMM 31219-189) with R and L P^3-M^3, and a badly crushed skull(TMM 31219-224) of an old individual. The skull is small, the basal length of the senile specimen is approximately 26. The snout appears narrow and long, but this may be due to the age and state of preservation of the specimen. The ascending premaxilla is slightly concave or almost straight, and rises slowly to meet the nasals. The dorsal suture with the nasal is long, + 2.8, and the posterior suture with the maxillar bone is vertical or slightly longer dorsally. The free part of the nasals is short, 1.6, and bluntly pointed. The facial crest reaches as far anterior as M^1 in TMM 31219-189, and M^1-M^2 in the senile specimen (-224). In the first specimen the ventral part of the lacrimal fossa can be seen on the R side. Its posterior end, which is marked by a sharp, rounded edge, lies 3.8 over the anterior termination of the facial crest, and 1.1 posterior of the infraorbital foramen. In the senile specimen the fossa is harder to discern, due to the crushing and due to the lack of a marked posterior edge. It lies beneath the nasals, and runs along the suture of the nasal and maxillar bones, beginning slightly posterior of the point where these sutures meet the lacrimal bone. The length of the fossa is + 4.5. In this skull there seems to be a masseteric fossa just beneath the lacrimal fossa, between the orbit and the infraorbital foramen; Webb (1969) described a similar faint masseteric fossa in *Pseudhipparion retrusum* from Burge. The outlines of neither fossa are very clear, and the fossae are very shallow in the senile specimen; in the other skull the existence of a masseteric fossa cannot be determined due to reconstruction of that part of the face, but the lacrimal fossa appears rather well defined ventrally.

The infraorbital foramen is situated over P^4, and the anterior palatine foramen opposite M^3. Due to crushing and restoration the other cranial foramina are hidden or so strongly displaced as to make observations impossible.

Limb bones. The referred first phalanx is smaller than in *M. vetus,* but has the same proportions. The V-scar is short and raised; the central scar is not well defined and seems to be absent. There are lateral volar scars.

Discussion. Leidy (1873) figured (plate 20, figs. 14, 15) and discussed (p. 247) briefly some upper teeth from Washington County, Texas, which had been found at a depth of 25-30 feet when digging a well. He referred them to the species *Hipparion speciosum,* originally known from the Bijou Hills of South Dakota under the name *Hippodon speciosus* Leidy. Osborn (1918) and Stirton (1940) agreed that the type of *Hippodon speciosus* is not referable to *Hipparion,* and regarded it as indeterminable. Leidy (1873) identified the teeth from Washington County with *Hipparion* on the basis of the disconnected protocone and complicated enamel. These specimens correspond closely to *Merychippus* sp. A third specimen (Leidy, 1873, plate

20, fig. 17) found at the same locality may represent *Calippus francisi*, which would suggest a CS assemblage.

Merychippus republicanus (in Osborn, 1918) is similar to *M.* sp. in the numerous enamel plications on the wear surface, in the high frequency of plis dihypostyle, in the tendency for the postfossette to open into a hypostylar fossette, in the long, lingually indented hypocone, and in the bifurcated pli caballin. It probably differs in the shorter spur on the longer protocone and in larger size.

Both *M. relictus* and *M. precocidens* are rather small forms with isolated protocones. The protoconal spur in *M. relictus* is very short; *M. precocidens* lacks a spur (Russell, 1933). In both forms the plication frequency appears to be considerably lower than in *M.* sp. *Merychippus paniensis* also retains an isolated protocone almost to the base of the tooth, but the protocone seems shorter and rounder than in *M.* sp. The plication count, too, is lower in *M. paniensis*.

Simpson (1930) described a maxillar fragment with P^4-M^3 from Cummer Phosphate Mine, Newberry County, Florida, as a new species, *M. westoni*, which he separated from *M. gunteri* on the basis of the disconnected protocone (except in M^2) of the worn teeth. In *M. gunteri* from B and CS the protocone may remain disconnected almost to the base; however, the type teeth of *M. westoni* differ from teeth of *M. gunteri* in the absence of pronounced ribbing of the paracone and metacone, and long protocone compared to the length of the teeth. In these characters, *M. westoni* is advanced and resembles *M.* sp. from CS. The teeth of *M. westoni* are slightly smaller than most specimens of *M.* sp., and approach *C. francisi* in size.

Quinn (1955, pp. 42-43) mentioned "*Griphippus*" *(=Pseudhipparion)* in the CS fauna; without giving a specific description he thought that the material, a skull and jaw (TMM 31183-41) not available to me, belongs to a form probably ancestral to *P. gratum* and *P. retrusum*. *Merychippus* sp. resembles *Pseudhipparion* in the morphology of the lower cheek teeth, especially in the tendency of the metaconid to fuse anteriorly with the paralophid, leaving an isolated metaflexid lake, and in the obliteration of the entoflexid, characters also frequently noticeable in *Calippus*. In the lower premolars the metaconid-metastylid column is connected to a narrow stalk, and the pli hypoconid and parastylid are well developed in both *M.* sp. and *Pseudhipparion*. *Merychippus* sp. differs from *Pseudhipparion* in consistent late connection of the protocone to the protoconule, in the failure of the protocone to connect to the hypocone before the tooth is much worn, and the infrequent closure of the hypoconal groove in a lake. In these characters *M.* sp. rather resembles *Hipparion* and *Nannippus*. Stirton (1940) considered *M. insignis* the ancestor of *Nannippus* and *Hipparion*, and *M. republicanus* the ancestor of *Neohipparion;* both species are larger and more hypsodont than *M.* sp., which is morphologically closer to the small, low-crowned merychippines of the *M. gunteri* group. *Merychippus* sp. has many characters in common with the hipparions, and would make a suitable ancestor of these horses.

Merychippus sp.

Table 15

Occurrence. Lapara Creek fauna, Clarendonian of Texas Gulf Coastal Plain.

Material. TMM 30936, Site 8, George West, Live Oak Co.: Nos. 414 L lower M, 415 L lower P; TMM 30904, 1 mi E of George West, Live Oak Co.: No. 1 L M^3 and upper P; TMM 31132, Site 17, Bee Co.: Nos. 76 R upper M, 498 R lower P, 149, 419 R and L M^3; TMM 31170, Site 19, Bee Co.: Nos. 92N, K R and L upper P, 35 L P^2 or D^2; TMM 31081, Site 15a, Farish Ranch, Bee Co.: No. 954 R P^2.

Description. A few isolated teeth in the collections from LPC indicate the presence of a low-crowned *Merychippus.* The presence of this genus in faunas with advanced horses has been reported earlier (Gregory, 1942, Webb, 1969), and they probably represent the last holdovers from the Miocene.

The tooth crowns are low; maximum mesostylar height observed in two unworn or little-worn M^3 (TMM 30904-1, 31132-419) is 2.52 and 2.53, and in a lower premolar (TMM 30936-415) the metaconid height is 2.62. This is little more than the height of the crowns in *M. gunteri.*

The protocone is short and disconnected in early wear, with a prominent spur directed toward the protoconule. The hypocone is short, with a lingual indentation and hypoconal groove partly closed posteriorly by a pli dihypostyle. The groove, however, remains open to the base of the tooth.

The plication frequency is medium to rather high. In the premolars there is a tendency for the anterior fossette to remain open in the postprotoconal valley and, especially in P^2, for the fossettes to be interconnected.

The lower teeth resemble those of *Merychippus* in earlier faunas. The protoconid and hypoconid have rounded enamel borders, the metaconid-metastylid column is short, and the flexids simple. There is a pli hypoconid, but a parastylid is absent.

Discussion. Webb (1969) identified *Merychippus* cf. *insignis* in the Burge and, tentatively, in the Minnechaduza fauna. The teeth in that sample are much higher crowned than the Texas specimens; Webb (p. 78) gave 3.20-3.50 as the height of the teeth he studied. Length and breadth of the teeth in my sample fall inside the range of the sample of *M.* cf. *insignis.*

Genus *Calippus* Matthew and Stirton, 1930

Genotype: *Protohippus placidus* Leidy, 1869

Calippus francisi (Hay), 1924

Tables 16, 33; Fig. 4

Merychippus francisi Hay, 1924

Type. L upper molar, TAM 2390, from Noble Farm, Grimes Co., Tex. (Hay, 1924, Pl. 1, figs. 28, 29).

Occurrence. "Younger" B and CS faunas, Lower to Middle Barstovian of Texas Gulf Coastal Plain; Barstovian of Great Plains.

Material. "Younger" B: TMM 31162, gravel pit 15.5 mi E of Brenham, Washington Co.: No. 4 L upper P or M; TMM 40070, Summer's Pit, Washington Co.: Nos. 5, 13, 2L lower M, 5 R P_2, 27 L M_3, 26 R upper M, 1 L upper P, 13 L M^3, 31 phalanx I; TMM 40189, Farm Rd. 1370, Washington Co.: No. 1 R lower M; Cold Spring: TMM 31262, road cut 1 mi. N of concrete, De Witt Co.: no no. L lower P; TMM 31191, Site 2, San Jacinto Co.: Nos. 17 L M_3, 18, 29 R and L upper M, 12 L upper P or M; TMM 31219, Site 3, Jim Donahoe Farm, San Jacinto Co.: Nos. 240 L P_4-M_3, 212 R and L rami with P_2-M_3, 52, 147, 168, 172, 202, 283 3 R and 3L P_2, 11, 63, 82, 95, 106, 110, 122, 147, 164 3L and 7R lower M, 10, 52, 147, 164, 166, 196, 202 3R and 7L lower P, 110, 127, 196, 202 L and 4R M_3, 2, 6, 53, 62, 67, 81, 96, 121, 133, 139, 143, 158C, E, 173, 176, 8R and 10L upper M, 25, 67, 139, 143, 146, 158H, 165 4R and 5L upper P, 62, 67, 139, 143, 167, 197 3L and 3R M^3, 143 R P^2, 112 upper D, 117 phalanx I; TMM 31183, Site 2, Polk Co.: Nos. 63 palate with R and L P^2-M^3, 49 R ramus with P_2-M_3, 65 L M^3, 91 L upper M; TMM 31272, 4 mi SE of Chapel Hill, Hwy 290, Washington Co.: Nos. 4 L upper M, 35 R upper P, 10 L lower D, 38 L P_2, 1 R lower P, 37 R lower M; TMM 31245, 1 mi S of Holman, Fayette Co.: No. 10 L juvenile ramus with D_4, 4 L M^3; TMM 31085, Noble Farm, Grimes Co.: No no. 5L lower M, TAM 2543A L M^3, L P_2, L upper P or M, L upper M, R and 2L upper P, TAM 2390 L upper M (type *Merychippus francisi* Hay), TAM 2734 R lower P; TMM 31242, Site 4, San Jacinto Co.: No. 2, 17, 63 3 calcanea; TAM 2543, Loc 19, Barry Farm, Grimes Co.: R upper M (cast); TAM 2540, Cold Spring: R D_2, R lower M, L lower P, TAM 2539 R upper P, 2R and 4L upper M, R M^3; TAM 2570, Diamond Mtn., Montgomery Co.: L M^3, R lower P; TAM 2876, Mound Creek: phalanx I; TAM 2545A (unknown): 4R and 4L lower M, L M_3.

Diagnosis. Quinn (1955, p. 27, revised): small. Upper teeth slightly curved and hypsodont but lower than in later species, and expanded enteroposteriorly at summit of crown. Enamel pattern more complex than in later species; protocone of molars grooved at summit of crown; hypostylar fossette present; hypoconal groove open about halfway down the crown on the premolars and lower on the molars. Lower teeth with prominent parastylid; pli hypoconid present and traces of a pli caballinid may occur in the premolars. Hypoconulid of M_3 with deep internal groove.

Description. This horse occurs both in B and CS. In the earlier fauna it is rare, but it is common in CS. The type upper molar is characteristic of the species, but the referred upper P^2 (Hay, 1924, plate 2, figs. 1 and 2) does not belong to *Calippus francisi.*

Calippus francisi was described in detail by Quinn (1955) on the basis of a well preserved palate (TMM 31183-63) and jaw (TMM 31183-49). The teeth of *C. francisi* in this material form a homogenous sample in size and morphology, and conform with Quinn's description. The few teeth in B are little, if any, different from the specimens of CS age, and are already fully as hypsodont.

The protocone is narrowly connected from early wear on; it is long and lingually concave or flattened even in much-worn specimens (table 22). In P^2 the protocone may remain isolated until the tooth is worn. In a few specimens the protocone may also connect to the hypocone; all such cases are worn down to at least half the original height, but the protocone does not consistently connect to the hypocone even in much-worn teeth. The plication frequency is medium, although higher than in younger calippines (Quinn, 1955); in the sample at hand the range is 0-14 (table 22). The pli caballin is well developed in little-worn teeth, but tends to disappear with increased wear in the molars. Even in much-worn premolars the pli caballin is frequently still visible.

The hypocone is long and narrow with a lingual indentation, especially in the premolars and in the little-worn molars. The hypoconal groove has a strong tendency to close, forming a lake, which obliterates with increased wear. A hypoconal lake may form already at a mesostylar height of 2.50, i.e., at barely one-fourth of the crown worn down. The lake obliterates earliest at a height of about 1.25, but in a few specimens the hypoconal groove can be traced to the base of the tooth. There is a hypostylar fossette.

In the lower teeth the metaconid and metastylid are usually of equal size in contrast to younger species of the genus in which the metastylid is smaller (Quinn, 1955). In the premolars the metaconid-metastylid column connects to a narrow stalk, although in rare instances the labial groove reaches deep in between the metaconid and metastylid. In P_2 the column is sometimes simple. There is almost always a pli hypoconid and a simple entoconid spur. The paralophid may occasionally bear plications directed posteriorly into the metaflexid, as in *Merychippus* sp. from B and CS. As in that species the flexids tend to obliterate with wear; in the premolars the metaconid may fuse with the paralophid, leaving the metaflexid as an enclosed lake.

Milk teeth. Quinn (1955, fig. 2D) figured a deciduous D^3 or D^4 (TMM 31219-112) from CS, which he identified with *Nannippus.* The tooth is little worn, but some advanced characters, such as the closed crochet, well developed pli caballin and plications of the metaloph, are visible. The protocone is still disconnected; it is short and has an anterior spur. I refer this specimen to *C. francisi* because of its small size, the slightly larger, worn specimen (TMM 40070-5) referred to *M.* sp., is morphologically similar, except that the protocone is connected.

The lower milk teeth have feebly developed cingular structures; although the parastylid may be present, the protostylid is weak or absent, and the hypostylid is wanting.

Limb bones. The limb bones from B and CS tentatively referred to this species are small and delicate. The medial proximal phalanx is considerably longer than the phalanges of *Parahippus leonensis,* but about as narrow. The volar V-scar is short and pointed, and there is a long, narrow scar for the central ligament.

Discussion. The ancestry of *C. francisi,* the earliest representative of the genus, is unknown. Webb (1969, p. 82) mentioned that *C. francisi* is well represented in the Valentinian Niobrara River fauna, which also has been thought of as the source of the type of *C. placidus;* however, Webb thought that the latter was probably found in the Minnechaduza. Equally small, hypsodont forms with long, narrow protocones are not known until later, and then probably are the descendants of *C. francisi.* Some of the small, early, relatively brachyodont species of *Merychippus (gunteri, primus, tehachapiensis)* may have precociously connected protocone, but all have larger and especially broader teeth than *C. francisi.* Stirton (1940, p. 188) mentioned *Protohippus patruus* as being close to the line leading to *Calippus,* but that species, too, is larger than *C. francisi,* although not much larger than *C. placidus. Protohippus patruus* also seems too late in time to be more closely ancestral to *Calippus* than to other advanced *Merychippus (Protohippus),* such as *P. perditus* and *M. sejunctus.*

A progressive decrease in size from the oldest to the youngest species in the *Calippus* lineage has been proposed (Matthew and Stirton, 1930, Stirton, 1940), but later doubted by Quinn (1955, p. 40), who maintained (p. 66) that *Calippus* evolved from still smaller forms of *"Hippodon" (Parahippus,* part + *Merychippus,* part) and *Archaeohippus.* In fig. 3 he derived *Calippus* from *"Hippodon vellicans" (= Parahippus leonensis* in this work) as represented in GG, but this horse is larger than *C. francisi.* Before *C. francisi* no equally small, advanced forms are known, and LPC *C. regulus,* which Webb (1969) considered a probable descendant of *C. francisi,* is considerably smaller than its ancestor. Thus it seems that *C. francisi* was the descendant of some larger form, and became the ancestor of a still smaller species, *C. regulus.* At the same time there seems to have been a geographic size trend. Webb (1969, p. 81) commented on the slight difference in morphology between contemporaneous *C. placidus* and the much smaller *C. regulus,* and tentatively suggested this to be a consequence of Bergmann's effect.

Calippus francisi is an immigrant in the Gulf Coastal Plain faunas. The material furnishes only a short glimpse of the evolution of the genus and thus gives little significant contribution pro or con in the discussion of possible progressive dwarfing.

Calippus regulus Johnston, 1937

Tables 17, 34; Fig. 6

Calippus anatinus Quinn, 1955

Type. R upper tooth row with P^2-M^3, Panhandle-Plains Historical Museum no. 878, from Grant Lease, near Goldston, Donley Co., Texas.

Occurrence. Lapara Creek fauna, Clarendonian of Texas Gulf Coastal Plain and Texas Panhandle.

Material. TMM 30936, Site 8, 13 mi. SE of George West on hwy 202, Live Oak Co.: Nos. 153 R ramus with P_2-M_3, 219-222 R P_3-M_2, 31 L P_4-M_3, 99 R ramus with P_4-M_3, 156 R P_2, 379, 218, 377, 376 2R and 2L M_3, 71, 176, 373, 157, 155, 82 6R lower M, 82, 226 R and 2L lower P, 70, 138, 261 L and 2R P^2, 79, 198 R and L M^3, 70 R upper P or M, 70, 145, 352, 328, 354 L and 4R upper M, 70 2R and 2L upper P, 120 2 astragali; TMM 31132, Site 17, Bridge Estate, Bee Co.: Nos. 461 L ramus with P_2-M_2, 93 L ramus with P_2-P_3, 195 L ramus with P_2-M_3, 100, 108, 443, 148, 370, 229 5L and 2R P_2, 89, 65, 409, 229, 290 2L and 4R M_3, 63, 100, 491, 443, 188, 182, 240, 434, 443, 119, 25, 89, 116, 254, 527, 229 5R and 15L lower P, 44, 50, 443, 534, 100, 107, 108, 114, 135, 225, 323, 382, 353, 136, 98, 229, 421, 425, 466 8R and 16L lower M, 556 L P_3 and P_4, 26, 424 L and 2R P^2, 26, 78, 146, 225, 159, 122, 145, 352, 440, 559 5L and 5R upper P, 97,

TABLE 15.–STATISTICS OF THE TEETH,
MERYCHIPPUS sp., LPC

Variate	N	M	OR
P^3-M^2 length	4	1.82	1.62- 1.94
Br.	2	2.12	1.99, 2.24
P_3-P_4 length	2	1.84	1.73, 1.94
Br.	2	1.24	1.22, 1.26
M_1-M_2 length	1	1.79	
	1	1.26	

TABLE 16.–STATISTICS OF THE TEETH,
CALIPPUS FRANCISI, B and CS

Variate	N	M	σ	V	OR
P^3-M^2 length	38	1.37 ±.013	0.080	5.84	1.20- 1.51
Br.	29	1.64 ±.011	0.057	2.45	1.53- 1.76
P_3-P_4 length	14	1.49 ±.020	0.074	4.96	1.21- 1.61
Ant. br.	11	0.96 ±.021	0.070	7.29	0.88- 1.07
Post. br.	14	1.01 ±.019	0.071	7.05	0.88- 1.11
M_1-M_2 length	18	1.34 ±.017	0.073	5.46	1.05- 1.48
Ant. br.	18	0.86 ±.015	0.065	7.57	0.75- 0.95
Post. br.	18	0.78 ±.014	0.058	7.48	0.69- 0.92

TABLE 17.–STATISTICS OF THE TEETH,
CALIPPUS REGULUS, LPC

Variate	N	M	σ	V	OR
P^3-M^2 length	75	1.17 ±.010	0.085	7.22	0.94- 1.40
Br.	55	1.41 ±.016	0.118	8.33	1.10- 1.70
P_3-P_4 length	38	1.24 ±.011	0.068	5.44	1.05- 1.35
Br.	35	0.83 ±.009	0.055	6.68	0.65- 1.00
M_1-M_2 length	47	1.20 ±.013	0.092	7.67	1.00- 1.45
Br.	44	0.76 ±.009	0.061	8.01	0.65- 1.00

171, 288, 225, 279, 339, 398, 407, 442, 352, 499, 146, 569, 587, 598, 548 10L and 10R upper M, 76, 217 2L upper D, 127, 136, 442, 501 4R M^3, 324, 352 L and R upper P or M, 109 phalanx II, 518 MT III proximal fragment, 516, 565 2 astragali; TMM 31170, Site 19, Bee Co.: no no. R ramus with P_2-M_3, nos. 5L P_2-M_2, 51, 77, 39, 89, 119 3R and 4L lower M, 18, 50, 76 3R and 2L upper M, 38, 76 2R upper P, 76 L upper P or M, 39, 89 L and 3R lower P; TMM 31184, Site 18, Bee Co.: Nos. 7 R ramus with P_2-M_3, 15, 5 L and R lower M; TMM 31081, Site 15a, Farish Ranch, Bee Co.: Nos. 711 R and L P^2-M^3, 714 L ramus with P_4-M_3, 1160, 1290 R and L P_2, 1160 2L M_3, 661 L lower D, 51, 1160 2L lower M, 863, 920, 1160, 1358 R and 3L lower P, 132 L M^3, 328 R upper P, 1122, 374, 1042 L and 2R upper M, 861, 1295 MT III and MC III, 304 proximal MT III, 1109, 1519 2 astragali, 817, 1074 2 calcanea, 323 Phalanx II; TMM 30896, Site 1, Buckner Ranch, Bee Co.: Nos. 173 juvenile skull with D^2-M^1 (type *Calippus anatinus* Quinn), 356, 361 L and R P_2, L P^2 and L M^3, 462 L M_3, 356, 360, 369E, 402 2L and 3R lower P, 341A, 356, 462, 538 5L lower M, 361, 551 L and 3R upper M, 361F, 551 L and R upper P, 361 L upper P or M.

Diagnosis. Very small, very hypsodont. Protocone connected from summit down, transversely oblique, not connecting to hypocone. Plication count low, incipient pli caballin in premolars disappears with wear, none in molars. Hypoconal lake closes early and soon obliterates completely. Lower cheek teeth with short metaconid-metastylid column; metaconid usually longer than metastylid. Premolars with shallow labial groove and long comissure, molars with deep labial groove.

Description. Webb (1969, p. 82) in his discussion of *Calippus placidus* from Minnechaduza synonymized Quinn's species *C. anatinus, C. optimus,* and *Astrohippus curtivallis* under the name *C. anatinus.* He pointed out that the types of these taxa differ from each other mainly in characters that change with wear. The material that Quinn (1955) referred to *C. optimus* and *C.* cf. *placidus* falls in the upper part of or outside the size range of the *Calippus* sample, and I believe that Quinn probably misidentified specimens of *Pseudhipparion* sp., which except for being slightly larger than *C. regulus* in mean size, is very similar to that species. I consider all specimens described and figured in Quinn (1955, Plates 6 and 7) as *C. optimus, C.* cf. *placidus,* and *Astrohippus curtivallis* as belonging to *Pseudhipparion,* and *C. anatinus* a synonym of *C. regulus* Johnston.

Quinn (1955) gave detailed descriptions of individual teeth of each new species of *Calippus* in LPC, and compared the Texas Gulf Coastal Plain forms with *C. placidus* and *C. regulus.* Webb (1969), too, found differences between *C. anatinus* and *C. placidus.*

The protocone is connected to the protoconule already in beginning of wear. In two specimens it is only barely connected. It is long (table 22) in comparison to the length of the tooth, slightly lenticular and pointed, and directed obliquely anterolabially. It does not connect to the hypocone even in much-worn teeth, although this is occasionally the case in *C. francisi.*

The hypocone is usually the size and shape of the protocone in the premolars, shorter in the molars. There may be a slight lingual indentation, which often disappears with wear. The hypoconal groove has a strong tendency to close, forming a lake, through the lingual extension of a pli dihypostyle. The lake may have formed already in the unworn tooth, but usually it forms soon after wear has begun or at a mesostylar height of 3.25-3.50. With continued wear the lake obliterates, until there are no traces of hypoconal markings. The lake may obliterate already at a height of 3.00, and at 2.50 or less it has always obliterated.

The plication frequency is low, about 50 percent of the teeth have a plication count of 0, none has a count of more than eight plications on the wear surface. There is usually a simple pli caballin in the premolars, but in the molars there is mostly none.

The metaconid is usually longer than the metastylid, but the difference is not pronounced in the premolars. The parastylid is well developed in both premolars and molars, and there is often a pli hypoconid in the little-worn teeth.

Milk teeth. Quinn (1955, p. 31) described the milk teeth of the type (TMM 30896-173) of *C. anatinus.* Not much can be added, except that the small, round fossette anterointernal to the prefossette of D^2, commented on by Quinn, is the remnant of an open connection through which the prefossette had opened anteriorly. This is rather common in D^2 in early wear of most of the horses in LPC.

The only lower milk tooth (TMM 31081-661) has a parastylid, but lacks a protostylid.

Limb bones. Postcranial material of this small horse is not common in LPC. Two metapodials are small and slender; MT III lacks a facet for the mesocuneiform.

In the referred proximal medial phalanx the V-scar is very short; the central scar is long in one specimen, in another it is weak. There are well developed lateral volar scars. These specimens differ from those of *Pseudhipparion* in considerably smaller size.

Discussion. Calippus regulus is the most hypsodont horse in LPC (table 23). Quinn (1955, p. 31) compared *C. anatinus* and *C. regulus,* and distinguished them on the basis of morphological characters, which he admitted differ in degree only. He considered the two species closely related. Webb (1969, p. 82) thought *C. anatinus* to be more primitive than *C. regulus* in several features of the upper teeth, among others the more complicated enamel pattern. The mean plication count in *C. regulus* from LPC is 2.19 ±.22, and thus close to a possible minimum, as also Quinn (p. 31) pointed out. Webb thought that *C. anatinus* further differs from *C. regulus* in that the hypoconal groove remains open or shows a lake later in wear. In the LPC sample the hypoconal groove may be closed already when wear begins, at a height of > 4.00; after that the lake obliterates and finally no signs of a groove are visible. At a height of 2.50 the groove is either closed or obliterated, and at 2.00 only few specimens show the lake.

Calippus regulus from the Clarendon differs from *C. regulus* in LPC in possibly slightly larger all over size. The teeth are almost the same size, but are more hypsodont, index 32.3. The protocone is as long (0.49 ± .004), but the plication frequency is a little lower (1.58 ± .12). In the upper teeth a hypoconal lake may have formed already at the summit of the crown, but I have also observed a lake in a specimen less than 1.75 high, i.e. at a later stage of wear than in the LPC sample. The hypoconal groove can be traced a little lower down on teeth in the LPC sample, or to 1.90 from the base of the enamel; in the Clarendon sample to 2.20. The protocone, as in the LPC sample, does not connect to the hypocone, but I observed one case of a disconnected protocone in close contact with the protoconule.

Calippus regulus is supposed to be descended from *C. francisi,* which indicates some reduction of size in the evolution of the genus. There was also considerable reduction of the plication frequency and some shortening of the protocone, probably as a consequence of the decreased size.

Genus *Pliohippus* Marsh, 1874

Genotype: *Pliohippus pernix* Marsh, 1874

Subgenus *Astrohippus* Stirton, 1940

Subgenotype: *Protohippus ansae* Matthew and Stirton, 1930

Pliohippus (Astrohippus) martini (Hesse), 1936

Tables 18, 35; Fig. 6

Calippus martini Hesse, 1936
Protohippus perditus, in Quinn, 1955
Pliohippus supremus, in Quinn, 1955, part
Hippotigris sellardsi Quinn, 1955
Hippotigris parastylus Quinn, 1955
Equus laparensis Quinn, 1955
Equus sp., in Quinn, 1955

Type. L upper dentition with P^2-M^3, UCMP 32814, from Cragin Quarry, Beaver Co., Oklahoma.

Occurrence. Lapara Creek fauna, Clarendonian of Texas Gulf Coastal Plain, Texas Panhandle, and Great Plains.

Material. TMM 30936, Site 8, George West, Live Oak Co.: Nos. 67 L lower D, 68, 146, 208 3L M_3, 61, 143 R and 2L lower M, 61F, G, 11, 133, 223, 256 3R and 5L lower P, 352 L P^2, 112, 192, 268 R and 2L M^3, 60, 160, 255, 269, 367 2L and 3R upper P, 66, 164, 304, 343, 360, 392 L and 5R upper M, 399 astragalus, 390, 391 2 phalanx II; TMM 40539, S. F. Austin Park: Nos. 1 2L upper M, 3 L upper P; TMM 31132, Site 17, Bridge Estate, Bee Co.: Nos. 244 R ramus with P_2-M_2, 459 L ramus with P_3-M_2 (type *Hippotigris parastylus* Quinn), 445 R lower D, L D_2, 358, 472, 312 R and 2L lower D, 272, 359 R and L D_2, 312 R P_2, 50, 285, 380, 349, 343, 335, 408 3R and 4L M_3, 252, 321, 408 L and 2R P_2, 50, 64, 253, 285, 239, 309, 349, 338, 335, 343, 400, 403, 430, 437 7R and 8L lower M, 39, 21, 51, 64, 335, 343, 408, 430, 441, 443 5L and 6R lower P, 24B, E, 94, 90, 147B, 209B, 284B, C, 334B, 348C, 366A, 376, 541, 569, 596 7L and 10R upper M, 24D, 95B, 125A, B, 152A, B, 190B, C, 209A, 224A, 284D, 344, 348A, 348B, 366B, 429A 7L and 9R upper P, 49, 24C, 542 L and 2R upper P or M, 2B, 104B, 147C, 223, 224E, 238, 376, 436A, 470 3L and 7R M^3, 99, 161C, 505 R and 2L P^2, 99, 129, 356, 477 4L upper D, 28 proximal MT III, 38 MC III, 15, 48 proximal MC III, 34, 75, 330, 360, 512 5 astragali, 302, 364 2 phalanx II; TMM 31170, Site 19, Bee Co.: Nos. 1 R ramus with P_3-M_3, 57, 72, 74 2L and 3R P_2, 13, 91 L and R M_3, 74 R lower D, 13, 55, 57, 74, 87 3L and 4R lower M, 56F L upper M, 57, 74, 97, 112 2L and 2R lower P, 56C, D, 73 L and 2R upper P, 12, 16, 56G R and 2L upper P or M, 59, 75 3R upper D, 379 3R upper D, 379 L D^2, 11 R M^3, 11 MT III, 22 calcaneum, 103 phalanx II; TMM 31184, Site 18, Bee Co.: Nos. 19 R lower D, 11 L lower M, 10 R upper P; TMM 31081, Site 15a, Farish Ranch, Bee Co.: Nos. 664 R ramus with P_2-M_3, 640 L ramus, 169, 211, 1070, 1744 L and 3R upper M, 115, 955, 1210 3L P_2, 302 L P_2-P_3, 129, 329, 1183, 1251 2L and 2R upper P, 705, 1206, 2L P^2, 168, 729 2L lower M, 260, 318, 862, 1012, 1203 L and 6R lower D, 906 L D_2, 70, 112, 168, 1253, 1387 L lower P, 1422, R upper P or M, 362 proximal MC III, 441, 974, 1148, 1058 4 MC III, 404, 508, 973, 752, 984, 1061 6 MT III, 1129 distal MC III, 289, 788, 885, 1053, 1300 5 astragali, 62, 193, 360, 590, 761, 1292, 1297, 1499 8 calcanei, 71, 787, 1236, 1521 4 phalanx II; TMM 30896, Site 1, Buckner Ranch, Bee Co.: Nos. 545 R and L rami with P_2-M_2, P_2-P_4, 127 R P^2-M^3, 541 L ramus with P_2-M_3, 195 L P^2-P^4 (type *Equus laparensis* Quinn), 476 R juvenile ramus with D_2-D_4, 499 L P^3-M^2, 501 L juvenile ramus with D_2-D_4, 248 R ramus with M_1-M_3, 206 R ramus with P_3-M_3, 207 R juvenile ramus with D_2-M_1, 503 R and L P^2-M^3 (type *Hippotigris sellardsi* Quinn), 355A, 418B, 556 R and 2L upper M, 558 R upper P or M, 418A, 557 L and R upper P, 420 2L lower M, 344E, 420, 405 2L and 3R lower P, 533 L P_2, 355B L P^2, 398, 420 L and R M_3, 355C L M^3, 460 L and R upper D, 353 L D_2, 348 6 astragali, 351A, B, D-G 6 phalanx II.

Diagnosis. Hypsodont, crowns little curved. Protocone long, wooden-shoe or sickle shaped in early, oval-rounded in late wear, seldom slightly heeled, occasionally disconnected with spur in early wear. Plication frequently moderate to low, pli caballin in premolars, none or soon obliterated in molars. Hypoconal groove seldom encloses a lake. Lower teeth with short metaconid-metastylid column, little lingual grooving; flexids simple. Parastylid variable, seldom a pli caballinid.

Description. Stirton (in letter to Wilson) commented on the similarity between upper teeth referred by Quinn (1955) to *Protohippus perditus, Hippotigris sellardsi, Equus laparensis,* and *Equus* sp., and regarded these teeth and the lowers of *Hippotigris sellardsi, H. parastylus,* and *H. clarendonensis* as belonging to a "small species of *Pliohippus* in the *P. martini* and *P. ansae* group." Webb (1969), too, pointed out the synonymy of these species, referring them to *Astrohippus sellardsi* (Quinn). He referred Quinn's *Pliohippus supremus, Hippotigris parastylus,* and *Dinohippus subvenus* to *Pliohippus supremus.* The material from LPC clearly indicates the presence of two pliohippines, but the specimens which Quinn identified as *P. supremus* are too small to fit the sample of *P.* cf. *P. supremus,* i.e. *"Dinohippus subvenus"* Quinn (1955, Plate 4, fig. 4), which probably belongs to the larger species. Part of the material of Quinn's *Equus laparensis* does not belong to the species represented by the type, as also Stirton (in letter) points out. The lower premolar (TMM 30896-454, Quinn, 1955, Plate 14, fig. 3) and the tooth row (TMM 30896-480, Quinn 1955, Plate 14, fig. 5) belong to *Neohipparion occidentale.* I regard the small pliohippine in LPC as *Pliohippus (Astrohippus martini* (Hesse), and *Astrohippus* as a subgenus of *Pliohippus* as it was origi-

TABLE 18.–STATISTICS OF THE TEETH,
PLIOHIPPUS (ASTROHIPPUS) MARTINI, LPC

Variate	N	M	σ	V	OR
P^3-M^2 length	78	1.84 ±.017	0.146	7.95	1.45- 2.15
Br.	59	2.24 ±.018	0.138	6.16	1.90- 2.55
P_3-P_4 length	29	1.90 ±.025	0.135	7.10	1.60- 2.25
Br.	32	1.16 ±.019	0.105	9.05	0.90- 1.45
M_1-M_2 length	34	1.77 ±.022	0.129	7.31	1.50- 2.05
Br.	31	1.13 ±.020	0.114	10.09	0.85- 1.30

nally described by Stirton (1940).

The teeth are hypsodont, slender, and rather straight. The parastyle is broad, often grooved at the top, and directed anterolabially or labioposteriorly. The mesostyle is high and pointed. There is an incipient metastyle in some specimens. The paracone and metacone are slightly ribbed, but the ectoloph appears quite flat.

The protocone is narrowly connected, sometimes disconnected in early wear. The protocone, which seems long (table 22) due to transverse flattening, is wooden-shoe or sickle shaped in early wear, with a pointed posterolabial tip and rounded, seldom slightly heeled anterior end. The lingual border is often flattened or slightly concave in early, flattened or convex in late wear. In late wear the protocone becomes rounded oval and more broadly connected. In the molars it frequently connects also to the hypocone; this may occur already at a mesostylar height of 3.00.

The hypocone is shorter than the protocone, especially in the molars. In the premolars there is often a lingual prehypoconal groove. The hypoconal groove is deep, but quickly becomes shallow. In many specimens there is a strong tendency to form a hypoconal lake already in early wear, but usually the groove obliterates gradually, without forming a lake. The groove sometimes closes just posterolingual of the hypocone because of a lingual extension of the hypostyle. In some specimens it can be traced to the base of the tooth. A common feature of M^3 is the postfossette opening through the hypoconal groove, and later the closed groove forms a part of the postfossette. This feature also occurs in *Calippus regulus, Pseudhipparion* sp., and *Pliohippus* cf. *P. supremus.*

The plication frequency is low (table 22); a pli caballin is developed in the premolars, but mostly absent in the molars although in early wear there is occasionally a well developed pli caballin. In some premolars there occurs a small posterior plication on the protocone-protoconule commissure. The fossettes are often narrow transversely in the premolars, with flattened labial and lingual borders; in worn molars the fossettes are open and rounded.

The lower premolars have the metaconid-metastylid column on a narrow stalk; the column is often wide and flaring. The molars have a low metaconid-metastylid column and deep labial groove. The metaconid is usually larger than the metastylid, although in late wear the difference in size may disappear. The metaconid in the molars is typically longer than the metastylid. There is a pli hypoconid in the molars, and sometimes in the premolars; in a few premolars I have observed an incipient pli caballinid. The parastylid is variable; in some specimens it is traceable only low down near the base or not visible at all, but in others it is well developed throughout the length of the crown.

The entoconid is oval in beginning of wear, rounded and large in worn premolars. It is directed anterolingually in the molars, anteriorly in the premolars, and has a short anterolabially directed tip. In worn teeth, especially molars, the hypoconulid is only little set off from the entoconid. In the little-worn premolars the metaconid, metastylid, entoconid, and hypoconulid may be isolated.

Milk teeth. The milk teeth may be confusingly similar to those of *Nannippus* and *Neohipparion,* but usually have a more "primitive" pattern. The protocone is connected in all specimens, sometimes through a narrow commissure. The hypoconal groove remains open or obliterates gradually. The plication frequency is lower than in the hipparions, and there is seldom a hypostylar fossette.

In the lower milk teeth the metaconid-metastylid column is relatively short. The metaconid is oval and larger than the rounded metastylid. The flexids are simple and become quickly shallower with wear, until they are almost obliterated. The entoconid is shorter than in the hipparions, and lacks a well developed tip. The posteriorly directed hypoconulid is separated from the entoconid only by a shallow groove, which tends to disappear. The labial borders of the protoconid and hypoconid are rounded. The labial groove is fairly broad, and shows a slight posterior groove marking off the metastylid labially.

The parastylid, protostylid, and hypostylid are variable. Usually the parastylid is well developed, but it may be absent; the protostylid and hypostylid are absent or weak.

Limb bones. The referred metapodials are as long (MT III 20-22) as those of *Neohipparion occidentale,* but more robust. The feet were tridactyl, as the cannon bones have well developed distal lateral protuberances for the side-metapodials. The facet for the mesocuneiform on MT III varies; in two specimens it is absent, in one the facet is small, and in one it is large. The proximal phalanx cannot be separated from those of *Neohipparion* and *Nannippus* on the basis of size and proportions. The spring mechanism of the monodactyl foot was not developed, and the ligamental scars are similar to those in advanced three-toed forms.

The limb bones are similar in size to those of *P. martini* from Minnechaduza, but in that sample the side-toes were already reduced and nonfunctional in locomotion, at least in most individuals, and the spring-mechanism was developed. The type MT III of *P. pernix* (Yale Peabody Museum No. 13007) falls in among these observations, and is considerably shorter than metapodials referred to *P.* cf. *P. supremus* from LPC.

Discussion. Pliohippus martini from the Clarendon is as large as the LPC form, but considerably more hypsodont as the index is 30.6. Protoconal length in that sample is the same, but the plication count is slightly lower (3.63 ± .17). Although I observed as many disconnected protocones in the Clarendon as in the LPC sample, disconnected protocones are, relative to sample size, not as frequent in the Clarendon. Stirton (1940) observed the protocone connected to the hypocone in only one heavily worn specimen, but this feature is quite common in teeth, especially molars, less than 2.00 high. It is very rare in less worn teeth, and I have seen only one case.

A hypoconal lake is as frequent in the Clarendon sample as in the LPC, but the groove may obliterate earlier. In teeth less than 3.00 high the groove is mostly obliterated, but in LPC this is the case in teeth 2.00 high or less.

Some observations on the metapodials from the Clarendon fall in among those referred to *P. martini* from LPC. As is the case with the LPC specimens, the facet for the mesocuneiform is variable and the side-toes appear to have been fully developed.

The morphological variation in the teeth of LPC *P. martini* spans that observed in species of different genera. *Pliohippus martini* resembles *Merychippus (Protohippus) perditus* in size and hypsodonty, but the crowns are not much curved. The narrowly connected, flattened protocone is similar, and so are the open, simple fossettes and frequent absence of a pli caballin in the worn molars, and the tendency for a hypoconal lake to form in some specimens. Hesse (1936, p. 54) considered *P. martini* so close to *M. perditus* "that if the lower teeth were unknown, the two would be considered the same." Stirton (1940, p. 190), however, pointed out that the jaw, which Hesse referred to *P. martini,* may belong to *Nannippus.*

Pliohippus martini resembles the more progressive *P. ansae* in the forming of an incipient heel of the protocone, but in *P. ansae* the heel persists longer than in *P. martini.* The protocone is slightly longer in *P. martini,* and seems relatively narrower than in *P. ansae.* The posterior tip is especially longer and narrower in *P. martini* than in *P. ansae.* I did not observe a single case of a disconnected protocone in the younger form. The enamel pattern of the teeth of *P. ansae* is simple, the plication count is 2.83 ± .52, a pli caballin is usually absent, and in the lower teeth the parastylid is weak or absent. In only one lower premolar of *P. ansae* did I see an incipient pli caballinid.

The characters which separate *P. martini* from *P. ansae* resemble *P. supremus.* The presence of teeth with a disconnected protocone in early wear is an outstanding similarity, but in *P. supremus* the tooth crowns are much curved, and although a pli dihypostyle may constrict the hypoconal groove posteriorly, Webb (1969, p. 88) did not observe a hypoconal lake in *P. supremus* from Burge.

In both the LPC and Clarendon samples of *P. martini* groups of teeth can be sorted out and placed in different taxa on the basis of their morphology. The smaller specimens generally resemble *Merychippus (Protohippus) perditus* in the tendency for the hypoconal groove to close in a lake, in the lack of a pli caballin in the molars, and in the pointed, thin styles of the ectoloph. A number of teeth, mainly the larger in the samples, resemble *P. supremus* in transversely flattened fossettes, lack of a hypoconal lake, presence of a pli caballin in the upper molars and persistence of the pli caballin in the premolars, and strong styles. The measurements on the type of *P. supremus* (in Osborn, 1918, fig. 118:2) fall in among these specimens. In the lower teeth smaller specimens lacking or with a weak parastylid may be separated from the larger specimens with a well developed parastylid, but there is no clear bimodality in size of the teeth, and other morphological characters are overlapping.

Although there may be slight temporal differences between the LPC sites, none of the tooth characters occur more frequently or at the exclusion of others at any one site, and the pooled-sample coefficients of variation for length and breadth of the upper teeth and for length of the lower teeth are normal for homogeneous samples; those for breadth of the lower molars and premolars are rather high.

Pliohippus (Astrohippus) martini may represent an extension of the evolutionary line from *M. vetus* through *M. circulus.* There are similarities in the rather straight crowns of the teeth, in the form and narrow connection of the protocone, which occasionally is isolated from the protoconule in early wear, in the flattened fossette borders of the premolars, and the narrow styles of the ectoloph. In *M. circulus* the hypocone does not enclose a lake, although there is a prominent pli dihypostyle, but gradually obliterates. An incipient pli caballinid does occur in *M. circulus* as in *P. martini.*

Subgenus *Pliohippus* Marsh, 1874

Subgenotype: same as genotype

Pliohippus (Pliohippus) cf. *P. supremus* (Leidy), 1869

Tables 19, 36; Fig. 6

Protohippus supremus Leidy, 1869
Pliohippus supremus, in Quinn, 1955, part
Dinohippus subvenus Quinn, 1955
?Asinus, in Quinn, 1955

Type. Two upper L molars of different individuals (Gidley, 1907, selected as the type Leidy, 1869, plate 27, fig. 4), in the Academy of Natural Sciences, Philadelphia, collections, from Little White River, S. D.

Occurrence. Lapare Creek fauna, Clarendonian of Texas Gulf Coastal Plain, Texas Panhandle and Great Plains.

Material. TMM 30936, Site 8, George West, Live Oak Co.: Nos. 61, 159, 386 3L M_3, 11, 203 R lower P, 17, 119 2 astragali, 232 calcaneum; TMM 31132, Site 17, Bridge Estate, Bee Co.: Nos. 444 R ramus with P_3-M_3, 333 R ramus with P_2-M_3 (type *Dinohippus subvenus* Quinn), 34, 86E, 110, 124, 313, 435 L and 5R upper M, 24, 41A, B, C, 51, 90A, 95A, 104A, 147A, 224B, C, 246, 267, 284, 378B, 429B, 435 7L and 10R upper P, 39, 57, 87, 80, 112, 285, 206, 237, 367, 380, 400, 437 5R and 10L lower M, 39, 55, 68, 252, 349, 486, 496 2R and 6L lower P, 77, 247, 270 L and 2R upper D, 173, 378A L and R P^2, 241, 278, 408, 506 R and 3L lower D, 68 L P_2, 102, 378D, 410, 475 4L D^2, 86D, 154, 246B, C L and 3R M^3, 68, 252, 321, 335, 349 2L and 3R M^3, 86A, C, 190, 194, 378C, 435 L and 5R upper P or M, 98, 197, 201, 463 4 MT III, no no. distal MC III, 75, 110, 140, 273, 1167 5 astragali, 218, 329, 390 3 calcanei, 219 phalanx II; TMM 31184, Site 18, Bee Co.: Nos. 9 L M_3, 18 R P^2, 8 L upper M, R upper P or M; TMM 31170, Site 19, Bee Co.: Nos. 10, 75 R and 2L upper D, 11 R upper P and L M^3, 13 R M_3, 24 MC III; TMM 31081, Site 15a, Farish Ranch, Bee Co.: Nos. 625 L upper P or M, 1251, 1513 L and R upper P, 426 MC III, 908 calcaneum; TMM 30896, Site 1, Buckner Ranch, Bee Co.: Nos. 502 R juvenile ramus with M_1-M_2, 188 L and R D^2-D^4, 158 R upper M, 348

TABLE 19.–STATISTICS OF THE TEETH,
PLIOHIPPUS (PLIOHIPPUS) cf. *P. SUPREMUS*, LPC

Variate	N	M	σ	V	OR
P^3-M^2 length	24	2.18 ±.021	0.104	4.77	2.00- 2.40
Br.	19	2.73 ±.032	0.138	5.05	2.40- 3.00
P_3-P_4 length	8	2.31 ±.044	0.124	5.35	2.15- 2.50
Br.	9	1.39 ±.039	0.118	8.45	1.20- 1.60
M_1-M_2 length	10	2.23 ±.061	0.192	8.61	2.00- 2.70
Br.	12	1.27 ±.025	0.087	6.81	1.15- 1.50

TABLE 20.–STATISTICS OF THE TEETH,
NANNIPPUS cf. *N. INGENUUM*, LPC

Variate	N	M	σ	V	OR
P^3-M^2 length	114	1.62 ±.006	0.096	5.93	1.40- 1.80
Br.	96	1.89 ±.013	0.132	7.01	1.50- 2.25
P_3-M_2 length	84	1.68 ±.010	0.091	5.43	1.50- 1.90
Br.	82	1.06 ±.010	0.091	8.62	0.80- 1.30

TABLE 21.–STATISTICS OF THE TEETH,
NEOHIPPARION OCCIDENTALE, LPC

Variate	N	M	σ	V	OR
P^3-M^2 length	95	1.89 ±.013	0.125	6.60	1.65- 2.20
Br.	85	2.12 ±.013	0.122	5.67	1.85- 2.40
P_3-M_2 length	78	1.94 ±.012	0.109	5.64	1.70- 2.20
Br.	73	1.16 ±.015	0.128	10.99	0.85- 1.45

TABLE 22.–PROTOCONAL LENGTH AND PLICATION COUNT. MEANS.

Species	Fauna	Protocone	Plications
Archaeohippus blackbergi	GG	0.25 ±.03	1.00
A. blackbergi	ThF	0.29 ±.007	2.83 ±.22
Parahippus leonensis	GG	0.42 ±.007	4.53 ±.26
P. leonensis	ThF	0.46 ±.003	4.15 ±.15
Merychippus gunteri	B & CS	0.56 ±.02	8.16 ±.84
M. vetus	B	0.64 ±.02	6.55 ±.56
M. circulus	CS	0.65 ±.01	5.49 ±.53
M. sp. near *Hipparion*	CS	0.56 ±.007	12.62 ±.46
Calippus francisi	B & CS	0.59 ±.01	6.25 ±.37
C. regulus	LPC	0.49 ±.007	2.19 ±.22
Pliohippus martini	LPC	0.74 ±.01	4.27 ±.31
P. cf. *P. supremus*	LPC	0.90 ±.02	3.43 ±.43
Nannippus cf. *N. ingenuum*	LPC	0.61 ±.002	12.09 ±.45
Neohipparion occidentale	LPC	0.78 ±.003	13.71 ±.58

TABLE 23.–HYPSODONTY INDEX

Species	Fauna	Mean length	Mean height	Index
Archaeohippus blackbergi	ThF	1.08 ±.004	0.79 ±.016	7.3
Parahippus leonensis	GG	1.42 ±.008	1.30 ±.028	9.2
P. leonensis	ThF	1.53 ±.005	1.45 ±.017	9.5
Merychippus gunteri	B & CS	1.50 ±.025	2.32 ±.108	15.5
M. vetus	B	1.66 ±.022	3.21 ±.063	19.3
M. circulus	CS	1.70 ±.016	3.83 ±.108	22.5
M. sp. near *Hipparion*	CS	1.54 ±.016	3.20 ±.203	20.8
Calippus francisi	B & CS	1.37 ±.013	3.15 ±.060	23.0
C. regulus	LPC	1.17 ±.010	3.57 ±.066	30.5
Pliohippus martini	LPC	1.84 ±.017	4.70 ±.164	25.5
P. cf. *P. supremus*	LPC	2.18 ±.021	5.65 ±.045	25.9
Nannippus cf. *N ingenuum*	LPC	1.62 ±.009	4.14 ±.079	25.6
Neohipparion occidentale	LPC	1.89 ±.013	4.92 ±.093	26.0

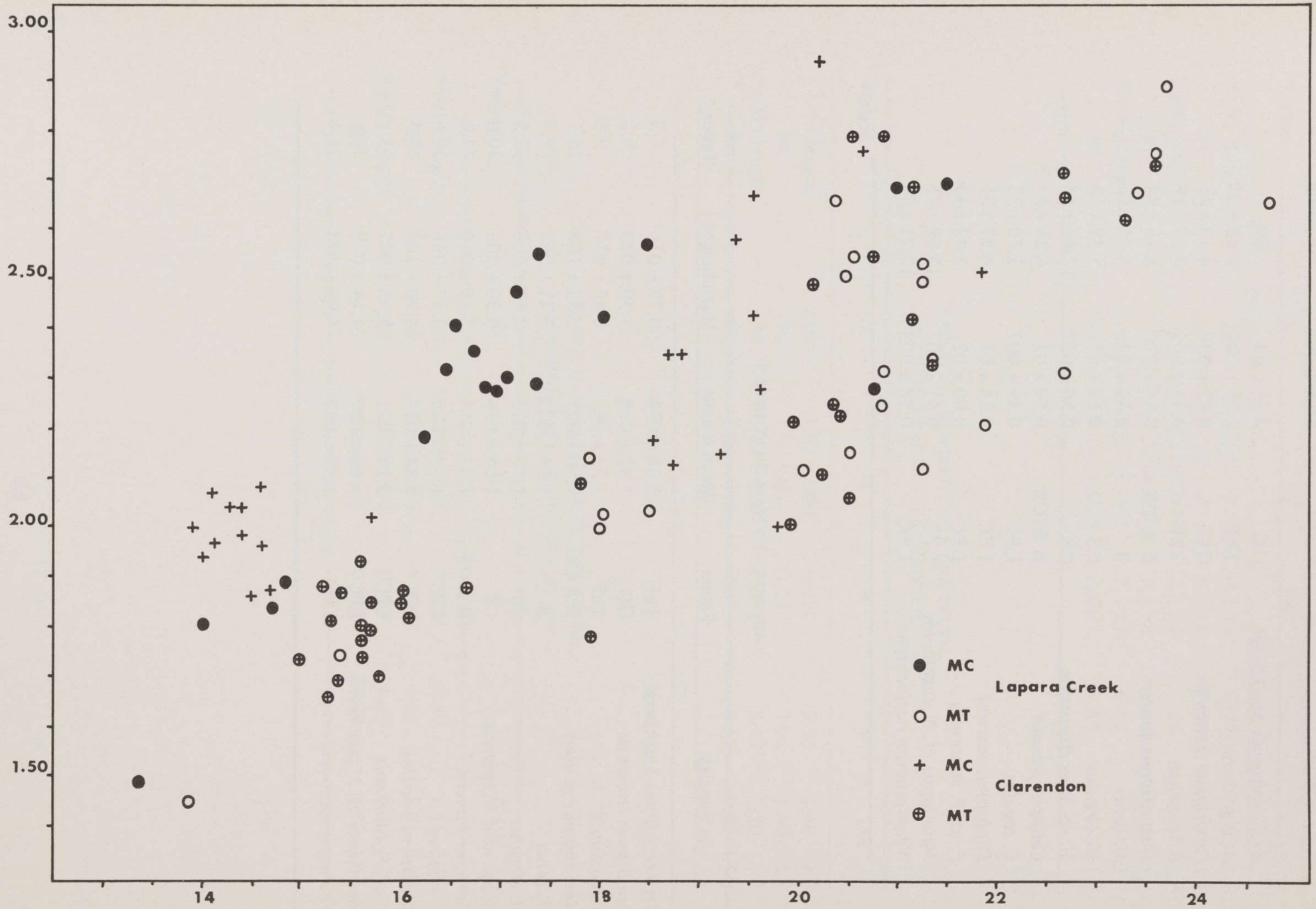

Fig. 6.—Relationship between length and distal breadth of MT and MC III in the samples from LPC and Clarendon. Vertical axis: distal breadth; horizontal axis: length. The length of MT III clearly shows six clusters of observations. The clustering of length of MC III is more diffuse owing to overlap between observations on *Nannippus* cf. *N. ingenuum*, *Pliohippus (Astrohippus) martini*, and *Neohipparion occidentale*.

astragalus, 373A calcaneum.

Diagnosis. (Leidy, 1869, according to Osborn, 1918): Superior molars resemble those of *Protohippus perditus;* protocone isolated in the unworn crown but early connected by wear with protoconule; prominent, simple enamel folds entering pre and postfossettes from metaloph. Pli caballin and prominent enamel fold into prefossette. Protocone elongate-oval, projecting farther inward than hypocone.

Description. Material in the LPC fauna suggest the presence of a large *Pliohippus.* Quinn (1955, pp. 43-45) described this form as a new genus and species, *Dinohippus subvenus,* but it is uncertain if it is validly different from earlier described forms of *Pliohippus.*

The parastyle may be heavy, sometimes with a central groove; the mesostyle is pointed, but is occasionally grooved close to the base. In some teeth there is a slight metastyle. The tooth crowns are strongly curved and expand toward the top.

The protocone is connected from beginning of wear. It is wooden-shoe shaped with convex labial and rounded, flattened or slightly concave lingual border. It connects to the protoconule through a narrow commissure, which often has a posteriorly directed pli protocone. The posterior tip of the protocone is pointed, the anterior end is often slightly expanded anteriorly. In much-worn specimens the protocone may also connect to the hypocone. One (TMM 31132-154) of the two M^3 has the protocone isolated, but in close contact with the protoconule.

The hypocone is slightly shorter than the protocone, and well marked from the metaconule by a lingual indentation and by the anterolingually directed hypoconal groove. The groove obliterates early, in all teeth with a height of less than 3.25 the hypoconal groove is obliterated. Quinn (1955) pointed out that in *"Dinohippus subvenus"* the groove swings lingually and closes just posterior of the tip of the hypocone. This is due to a lingual development of the hypostyle, similar to that observed in *Merychippus vetus* and *M. circulus,* and observed in *P. supremus* by Webb (1969). The groove seldom encloses a lake; I observed a hypoconal lake in only one specimen. There is often an open or closed hypostylar fossette.

The plication count is low (table 22). There is sometimes a pli caballin in the little-worn premolars, but with wear this soon disappears. The molars lack a pli caballin. In the premolars the postprotoconal valley reaches deep anterolabially toward the prefossette; occasionally this connection is open.

The lower cheek teeth have a simple and rather primitive pattern with rounded margins of the protoconid and hypoconid, and short and low metastylid-metaconid column separated by a shallow V-formed lingual and deep labial groove in the molars. There is only a faint or no parastylid. The molars in early wear may have a short pli hypoconid.

Milk teeth. The milk teeth resemble those of *P. martini,* but are more primitive in pattern. The parastyle is strong, flattened or slightly grooved. The mesostyle is pointed. The fossettes are simple and hardly plicated. The anterior fossette often opens into the postprotoconal valley as in the permanent teeth. The protocone is always connected already in early wear, and rather long. The hypoconal groove remains open or gradually closes.

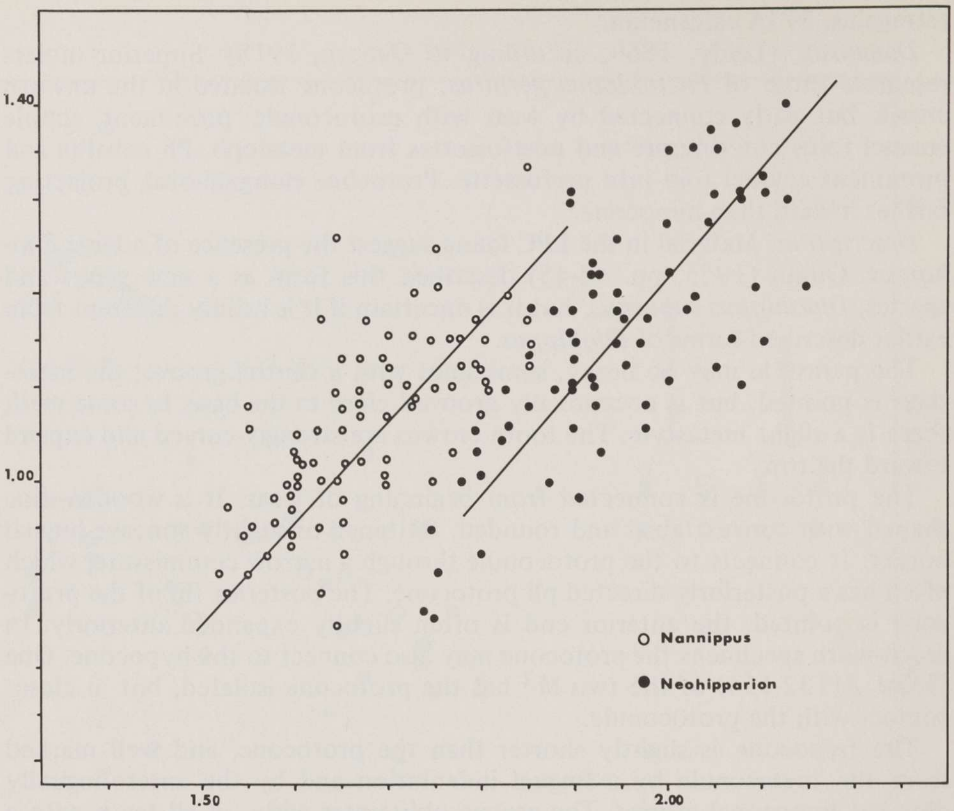

Fig. 7.—Relationship between length and breadth of P_3-M_2 in samples of *Nannippus* cf. *N. ingenuum* and *Neohipparion occidentale* from LPC. Vertical axis: breadth; horizontal axis: length. *Neohipparion occidentale* has relatively slightly narrower teeth than *Nannippus* cf. *N. ingenuum,* and there is little overlap of clusters.

In the lower milk teeth the metaconid-metastylid column is short, with a long metaconid and rounded metastylid as in the preceding species. The flexids are very simple and tend soon to obliterate, until only slight lingual grooves remain between the paralophid-metaconid and metastylid-entoconid.

The entoconid is very small and rounded in early wear, and lacks a tip. The hypoconulid is as in *P. martini.* The paralophid is low with a convex anterior border, as are the labial borders of the protoconis and hypoconid. The labial groove between the conids is broad and as in *P. martini* it shows a labial marking of the metastylid. There is usually a parastylid, and often a hypostylid, but a protostylid is absent.

In both the upper and lower deciduous teeth a cingulum may be present.

Limb bones. The referred metapodials are long (MT III 23- 25, MC III 20- 22), but not appreciably more robust than those of the other horses in the fauna. The stage of reduction of the side-metapodials appears to have varied. None of the four metapodials is unequivocally monodactyl. In all specimens the distal lateral protuberances, which support the distal end of the lateral metapodials with their phalanges, are well developed and rugose. In a couple of specimens, however, the side metapodials appear to have been

TABLE 24.–STATISTICS OF THE LIMB BONES,
ARCHAEOHIPPUS BLACKBERGI, GG

Variate	N	M	σ	V	OR
MC III length	2	9.58			9.38, 9.77
Prox. br.	1	1.12			
Prox. a-p.	1	0.91			
Dist. br.	1	1.08			
Tibia dist. br.	1	2.59			
Astragalus dist. br.	10	1.53 ±.049	0.156	10.2	1.21- 1.68
Height	9	2.18 ±.051	0.152	6.95	1.82- 2.31
MT III prox. br.	2	1.42			1.36, 1.48
Prox. a-p.	2	1.25			1.17, 1.32

connected to the cannon bone more intimately than is usual in three-toed horses. In those specimens the side metapodials are (TMM 31132-201) or appear to have been (TMM 31170-24) partly fused to the cannon bone. In all metapodials of the functionally three-toed horses I have seen, the side metapodials were probably connected to the cannon bone by interosseous ligaments allowing some inter-metapodial movement in locomotion. In recent *Equus* with its locomotively nonfunctional side-toes, fusion of the splints to the cannon bone is common. The occurrence of the facet for the mesocuneiform varies as in *P. martini.* This facet is absent in three specimens, but possibly developed in one.

A number of long, slender proximal medial phalanges are probably referable to *P.* cf. *P. supremus.* In some specimens the configuration of the volar ligamental scars indicate the incipient development of the spring mechanism of the monodactyl horses. In these specimens the V-scar is elongated, to one-third of the length of the bone, and flattened. The extent of the central scar varies: sometimes it continues distally from the lower tip of the V-scar, sometimes the central is covered by rugose extensions of the V-scar, and sometimes the V-scar continues distally, probably including the central scar. Lateral volar and central volar scars are variable.

Discussion. In size of the teeth this sample corresponds to Webb's sample of *P. supremus.* The teeth in the LPC sample are slightly higher crowned; mean height in eight unworn or slightly worn specimens in 5.65 ± .05, and disconnected protocones do not occur even in little-worn teeth, except M^3. The teeth from LPC further correspond to those from Burge and Minnechaduza in the strong curvature of the crown, expansion of the crown toward the top, shape and orientation of the protoconal commissure, and frequent occurrence of a pli protocone on the commissure. Webb did not mention the occurrence of the open connection between the anterior fossette and the postprotoconal valley in his sample of *P. supremus;* in one figured specimen (Webb, 1969, p. 86, fig. 24b) the protoconal valley reaches deep anterolabially toward the fossette, and seems to have been in contact with it at an earlier stage of wear. Webb described the styles of the ectoloph as heavy, but not grooved; grooving occurs occasionally in the LPC sample. The protocone in *P.* cf. *P. supremus* is considerably longer than in *P. supremus,* but the plication count is the same. In the lower teeth Webb observed an occasional pli hypoconid in some little-worn specimens, and well developed parastylids in the molars. In the LPC material parastylids are weak in both premolars and molars, a pli hypoconid occurs in the little-worn teeth, but a pli caballinid, which Webb observed in one case, is absent. In the size of the limb bones, too, *P.* cf. *P. supremus* corresponds to *P. supremus* from Burge and Minnechaduza.

Pliohippus cf. *P. supremus* differs from *P. simus* in larger size and higher crowns, in stronger curvature of the teeth, and more marked expansion of the crown toward the top. The fossettes of the upper teeth are more open and rounded, with concave labial and lingual borders, and there is no tendency for the anterior fossette to open in the postprotoconal valley in *P. simus.* The hypoconal groove closes earlier in *P.* cf. *P. supremus,* and does not tend to form a hypoconal lake. The protocone is longer and always connected to the protoconule. The lower cheek teeth with their rounded protoconid and hypoconid, and early obliteration of the flexids and of the lingual groove, seem primitive in pattern compared to *P. simus.*

Teeth of *Pliohippus* in the Clarendon material are as large and as hypsodont as those in LPC. The Clarendon teeth have a slightly shorter protocone (.85 ± .02) and lower plication count (3.24 ± .41). I have not observed a hypoconal lake, but in two uppers, one of which is M^3, the protocone is disconnected, although in close contact with the protoconule. In other features the Clarendon teeth are similar to those from LPC, for instance in the deep postprotoconal valley and the tendency of the posterior fossette of M^3 to open through the hypoconal groove. Some metapodials in the Clarendon sample fall within the specimens referred to *P.* cf. *P. supremus.* The facet for the mesocuneiform on MT III is variable, developed in two, absent in two specimens, and none of the metapodials belong with certainty to a monodactyl horse.

Webb (1969), following Stirton and Chamberlain (1939), synonymized most species of *Pliohippus.* He separated the known taxa into two categories: *P. supremus* with a well developed malar fossa on the face, and *P. pachyops* with no malar fossa. He did, however, list (table 1, p. 14) both *P. supremus* and *P. fossulatus* from the Clarendon. If skull material is necessary for an identification, *P.* cf. *P. supremus* cannot be identified with certainty, since cranial material is lacking. The skull (Plains-Panhandle Historical Museum No. 1105) of *Pliohippus* from Clarendon shows the wide preorbital fossa with an upper lacrimal part and two lower masseteric parts separated from each other by bony bars. Since the teeth and the limb bones in LPC resemble *Pliohippus* from Clarendon it may be supposed that LPC *P.* cf. *P. supremus,* too, had a well developed fossa.

Although *P.* cf. *P. supremus* resembles *P. supremus* from Burge and Minnechaduza the teeth do not correspond to the type of *P. supremus,* which is smaller and falls outside the range of *P.* cf. *P. supremus.* The Burge and Minnechaduza samples partly overlap both the type of *P. supremus* and LPC *P.* cf. *P. supremus,* but resemble *P. supremus* more closely morphologically.

TABLE 25.–MEASUREMENTS ON THE LIMB BONES, *ANCHITHERIUM NAVASOTAE*, GG

Number	Variate	Measurements
TMM 40067-57	astragalus, dist. br.	±3.24
	height	4.73

TABLE 26.–MEASUREMENTS ON THE LIMB BONES, *HYPOHIPPUS AFFINIS*, LPC

Number	Variate	Measurements
TMM 31132-75	astragalus, dist. br.	3.61
	height	5.03

Pliohippus cf. *P. supremus* approaches *P. interpolatus* in height of the tooth crowns and in size, and may have been evolving toward that advanced species, as Quinn (1955) recognized. The LPC sample resembles *P. interpolatus* rather than *P. supremus* in the tendency of the prefossette to open into the postprotoconal valley. *Pliohippus interpolatus* has a much shorter protocone and slightly higher plication count than *Pliohippus* from either Clarendon and LPC, and this horse is monodactyl and has a facet for the mesocuneiform on MT III and occasionally a facet for the trapezoid on MC III.

Genus *Nannippus* Matthew, 1925

Genotype: *?Hipparion venustum* Leidy, 1856

Nannippus cf. *N. ingenuum* (Leidy), 1885

Tables 20, 37; Figs. 6, 7

Hippotherium ingenuum Leidy, 1885

Type. Two L upper molars, U. S. National Museum No. 3306, from Alachua clays, or Archer beds, of Archer, Fla.

Occurrence. Lapara Creek fauna, Clarendonian of Texas Gulf Coastal Plain, Texas Panhandle and Florida.

Material. TMM 30936, Site 8, George West, Live Oak Co.: Nos. 65, 252, 364 3L upper M, 193 L P^2, 136, 363 2L upper P, 61 L P_2, 68 L lower D, 67, 133, 325, 345, 387, 388 2L and 6R lower M, 202, 215 L and R lower P, 63, 183, 227, 384 R and 3L M_3, 72, 154, 307, 365 L and 3R M^3, 361, 366 L and R upper P or M; TMM 40539, S. F. Austin Park: No. 2 R lower P; TMM 31132, Site 17, Bridge Estate, Bee Co.: Nos. 431 R ramus with P_2-M_3, 72 R ramus with P_2-M_2 and M_3, 462 L ramus with P_2-P_3, 2A, 43, 103A, 151, 161B, 189C, 22A, C, 307, 433B, C, D, 440, 600 7L and 8R upper M, 103B, 161A, 171, 178, 269, 235, 245D, 348D, 350A, 402, 440, 488, 547, 584, 605 7R and 9L upper P, 45, 81, 91, 172, 192, 230, 252, 287, 396, 441, 474, 552, 577, 578, 580 6L and 9R lower M, 10, 115, 287, 308, 380, 471, 503, 545, 559, 589, 592 6R and 7L lower P, 52, 440, 544 L and 2R upper P or M, 94, 169, 178, 269, 307, 536 2L and 4R P^2, 101, 156, 213, 227, 253, 338, 437, 509, 561 3L and 7R P_2, 49, 88, 113, 170, 265C, 440, 537, 585 3R and 5L M^3, 81, 134, 266, 300, 322, 396, 555, 581 4R and 5L M_3, 228 R D^2, 72, 325, 543 3L upper D, 422 L D_2, 354, 357 2L lower D; TMM 31170, Site 19, Bee Co.: Nos. 69H, 92F, G, J. 52, 71B R and 5L M^3, 70, 91 2R P_2, 70, 96, 117 L and 2R M_3, 101 R upper D, 97 L and R lower D, 52B, 54B, 69G, 90A, E, 92D, E, H. M, N. O, 111B 4R and 8L upper M, 90F, G, 92A, B, C, 92L, 111C 3R and 4L upper P, 17, 72, 91 4L and 4R lower M, 17, 55, 57, 91 3L and 3R lower P; TMM 31184, Site 18, Bee Co.: Nos. 11 2L lower M, R M_3; TMM 31390, 0.5 mi SW of Normana on Medio Creek: Nos. 2 L P_2, L lower P, 2R lower M; TMM 31081, Site 15a, Farish Ranch, Bee Co.: Nos. 675 L ramus with P_2-M_3, 303 L ramus with P_2-M_2, 334 R ramus with P_2-P_4, 27 R ramus with P_2-M_3, 501 R ramus with P_2-P_4, 411 L ramus with P_2-P_4, 1511 L ramus with P_2-M_1, 213 L ramus with P_4-M_3, 175 L ramus with P_2, 1035 R ramus with P_2, 176 R ramus with M_1-M_3, 1410 R P_2-P_4, 52, 72A, B, 222, 269, 330, 341A, B, 375, 630D, 658, 659, 672, 950, 952, 1033, 1118, 1159B, D, 1219, 1240, 1288, 1372A, E, 1392, 1397C, 1411, 1421, 1463 15L and 16R upper M, 50, 72C, D, 221, 319, 596, 628, 641, 660A, 786, 822, 825, 826, 1140, 1159A, C, 1397A, B, 1466, 1489, 1505 5L and 17R upper P, 95, 245, 246, 255, 290, 318, 650, 724, 794, 1031, 1043, 1252, 1423, 1424, 1464, 1512 7L and 10R lower M, 95, 168, 290, 598, 704, 707, 904, 953, 956, 1252 6L and 7R lower P, 44, 823, 1375, 1421, 1441 3L and 4R upper P or M, 379, 630B, 644, 660B, 1440, 1482 2R and 4L P^2, 397, 649, 715, 1253 R and 3L P_2, 222, 558, 628, 795, 824, 905, 1011, 1161, 1222, 1372, 1411, 1463, 1513 5R and 9L M^3, 51, 170, 557, 729, 1123, 1207, 1377, 1481, 1512 4L and 5R M_3, 53, 204, 341, 1119, 1282, 1292, 1371 4L and 6R upper D, 124, 917, 1291, 1425 L and 3R lower D, 1282 L D^2, 1506 L D_2, 421, 427, 442, 563, 564, 580, 1266 7 MC III, 420, 429, 440, 930, 1265 5 MT III, 733 distal metapodial, 1301, 1516 2 astragali, 589, 1132, 1188 3 calcanea; TMM 30896, Site 1, Buckner Ranch, Bee Co.: Nos. 414 R D_2, 360 L P_2, 344 2R lower P, 539 R M_3, 404 L upper D, 340A, C, D R and 2L P^2, 359, 537 L and 2R M^3, 450 L upper P and M, 204, 400 2R upper P or M; TMM 30898, Site 2, Buckner Ranch, Bee Co.: Nos. 6 L M_3, 8 R P^2, 10 R upper M.

Diagnosis. Hypsodont. Protocone lenticular or long-oval, with spur or anterolabially oblique in early wear. Plication count high; pli dihypostyle but no hypoconal lake. The crochet may remain disconnected in early wear. Lower teeth with wide, flaring metaconid-metastylid column; labial groove shallow or occasionally deep in premolars, deep in molars. Parastylid, pli caballinid, and additional plications in flexids common.

Description. The two hipparions in the LPC sample, *Nannippus* and *Neohipparion,* are very similar. There is broad overlap in size, and although extremes in size and morphology are easy to identify, a large number of specimens cannot with absolute certainty be referred to species. The pooled samples of teeth show high coefficients of variation, and distributions of measurements, especially on lengths, are clearly bimodal, indicating heterogeneity. The upper teeth of the two species were separated on the basis of size, absolute length of protocone, length of protocone to basal length of tooth, and plication frequency, no character of which is a fool-proof key. The lower teeth were discovered to differ in proportions; the teeth of *Nannippus* are proportionally broader, and there is not much overlap of scatters.

The styles of the ectoloph are thinner than in *Neohipparion,* but this may be a consequence of the smaller size. The mesostyle of the premolars is pointed, the parastyle faintly grooved. The mesostyle of the molars is thin and pointed, the parastyle broader and flattened, and slightly extended posteriorly. The interstylar valleys are flattened and ribbed.

The protocone is usually lenticular with pointed ends, sometimes rather long and flattened. In early wear it usually has an anterior spur directed toward the protoconule; sometimes the whole protocone is anterolabially oblique. It may also be markedly concave lingually. It does not connect to the protoconule until the tooth is much worn; teeth with a mesostylar height under 1.25 usually have a connected protocone. I have not observed the protocone to connect to the hypocone.

The hypocone varies in length, but is mostly rather short and lacks a lingual indentation in the molars. In the premolars there is sometimes a faint lingual indentation. The hypoconal groove is deep and remains open to the base of the crown. Although there is sometimes an apparent tendency for the groove to close, I have not observed a specimen with a hypoconal lake, except M^3 in which a hypoconal lake is fairly common.

The plication frequency is high. In some premolars in early wear there is a tendency for the prefossette to open lingually in the postprotoconal valley, i.e., for the crochet to remain disconnected; in this character *Nannippus* cf. *N. ingenuum* resembles *Neohipparion occidentale.*

The lower teeth resemble morphologically those of *N. occidentale.* In the premolars the tendency to form plications is not as evident as in that species, and although the pli caballinid is as frequent, it is shorter in *Nannippus.* In some premolars the labial groove is very deep, almost reaching the metaconid-metastylid commissure.

The upper teeth of *N.* cf. *N. ingenuum* differ, although only in degree, from those of *N. occidentale* in the generally lenticular protocone, simple hypocone, lower plication count, thinner styles, and less developed metastyle. Failure of the crochet to connect to the protoloph in early wear is also much more frequent in *Nannippus.* The lower teeth differ in less developed plications, including the pli caballinid, and stronger tendency of the metaconid to unite anteriorly with the paralophid, leaving the metaflexid as an enclosed lake in the worn molars.

Milk teeth. The protocone is usually isolated with a more or less pronounced spur, although in a few specimens it is connected already in early wear. The protocone is often connected in D^2. The hypocone may be isolated in early wear, and remains well set off from the metaloph by an anterior groove and by the hypoconal groove, which stays open to the base of the crown.

The plication frequency is high and is evidenced by multiple plis dihypostyle in the hypoconal groove. The prefossette often opens into the postprotoconal valley, and there is usually a hypoconal fossette, isolated or opening into the postfossette.

The lingual cingulum may be well developed.

In the lower deciduous teeth the metaconid-metastylid column is long; in early wear the metaconid tends to droop labially. The entoconid is long and pointedly oval, with a well developed anterior tip, sometimes almost reaching the bottom of the entoflexid. The hypoconulid is well set off from the entoconid by a marked lingual groove, and directed lingually or posterolingually.

There is always a strong parastylid, but the protostylid is variable; sometimes it is well developed, sometimes weak or lacking. There is occasionally a pli caballinid and a weak hypostylid.

Limb bones. The referred metapodials are shorter and proportionally slightly more robust than those of *N. occidentale.* Of four MT III, one lacks a facet for the mesocuneiform. The proximal phalanx is similar to that in *Neohipparion.*

The metapodials correspond in length and proportions to those of *Pseudhipparion retrusum* and *P. gratum* from Burge and Minnechaduza, but the phalanges, astragalus, and calcaneum are larger and broader.

Discussion. Webb (1969, p. 14) listed *Hipparion* cf. *plicatile* from the Clarendon type localities. In *H. plicatile* from Florida the protocone is oval with rounded edges and the plication count is very high (Osborn, 1918, figs. 55, 55a). The small hipparion in the Clarendon corresponds to *N.* cf. *N. ingenuum* in LPC in the lenticular protocone with a spur in early wear and in plication count. The protocone is slightly longer (.65 ± .01), but the plication count is almost identical (11.96 ± .62). The tooth crowns are higher, index 26.97, and length and breadth, too, are greater in the Clarendon form. A few metapodials in the Clarendon sample correspond to those referred to *N.* cf. *N. ingenuum.* Both MT III lack a facet for the mesocuneiform.

Hesse (1936) referred some material from the Beaver fauna to *Neohipparion* cf. *coloradense,* and Webb (1969, pp. 108-109) later identified this sample as belonging to *N. occidentale.* The rather lenticular protocone, simple hypocone, and small size of the teeth resemble those of *Nannippus* from LPC. Some larger specimens commented on by Webb may belong to *Neohipparion.*

Nannippus cf. *N. ingenuum* resembles *N. tehonensis* in the complicated pattern of the enamel, in the incipient metastyle (Drescher, 1941, p. 12), in the occurrence of a protoconal spur and the sometimes oblique protocone in the premolars, and well developed hypoconal groove. The height of the tooth crowns is also about the same in the two forms. Quinn (1955, p. 73) recognized this species in the LPC fauna together with *N. ingenuum.*

Nannippus lenticulare (Chicago Field Museum, P 27175) from the Optima fauna, Oklahoma, is smaller (teeth 1.34-1.62 long at the base) and very hypsodont. The form of the protocone, and the simple hypocone and hypoconal groove are similar to these features in teeth of *N.* cf. *N, ingenuum* from LPC. A R upper M^2 (Princeton University, Museum No. 12196, plaster

TABLE. 27–STATISTICS OF THE LIMB BONES,
PARAHIPPUS LEONENSIS, GG

Variate	N	M	σ	V	OR
Radius dist. br.	2	2.83			2.69, 2.97
MC III prox. br.	1	±1.61			+1.61
Prox. a-p.	1	1.32			1.32
Tibia dist. br.	1	3.84			3.84
Astragalus dist. br.	15	2.00 ±.025	0.097	4.85	1.85- 2.18
Height	16	2.86 ±.042	0.167	5.82	2.53- 3.14
Calcaneum height	2	5.59			5.46, 5.72
Tuber br.	2	2.01			1.97, 2.05
MT III length	3	15.1			14.2- 15.8
Prox. br.	5	1.97 ±.047	0.106	5.38	1.88- 2.10
Prox. a-p.	5	1.72 ±.051	0.115	6.69	1.57- 1.80
MT-MC dist. br.	15	1.72 ±.016	0.063	3.66	1.60- 1.80
Phalanx 1 dorsal length	4	3.02			2.74- 3.21
least br.	4	1.42			1.28- 1.57
Phalanx 2 volar length	4	1.93			1.80- 2.08
br.	4	1.46			1.43- 1.59

TABLE 28.–LIMB BONE MEASUREMENTS,
PARAHIPPUS cf. *P. TEXANUS*, GG

Number	Variate	Measurements
TMM 40106-63	Astragalus, dist. br.	2.30
	Height	3.46
TMM 40068-18	Calcaneum, height	7.27
TMM 40068-5	MT III prox. br.	2.49
	Prox. a-p.	2.15

replica of original in AMNH) of *N. montezumae* from Lacualtipan, Hidalgo, Mexico, is, although worn, 4.87 high and more hypsodont than the teeth from LPC. Length and breadth at the base of this tooth fall inside the range of variation of *N.* cf. *N. ingenuum*.

Genus *Neohipparion* Gidley, 1903

Genotype: *Neohipparion whitney* Gidley, 1903

Neohipparion occidentale (Leidy), 1856

Tables 21, 38; Figs. 6, 7

Hipparion occidentale Leidy, 1856

Type. Four R upper molars, 1 L upper molar, Academy of Natural Sciences collection, Philadelphia, from Little White River, S. D.

Occurrence. Lapara Creek fauna, Clarendonian of Texas Gulf Coastal Plain, Texas Panhandle and Great Plains.

Material. TMM 30936, Site 8, George West, Live Oak Co.: Nos. 135 L P^2, 8, 66, 326 R and 5L upper M, 66, 269, 368, 370, 371 3R and 4L upper P, 148 R P_2, 11, 67, 68, 133, 189, 191, 324 3R and 6L lower M, 67, 133, 140, 190, 224, 235, 334, 327, 260, 414 4R and 7L lower P, 133, 184 2R D_2, 369 L upper D, 64A-F, 147, 305 6R and 2L M_3, 66, 135, 358 3R upper P or M, 33 MC III, 394 astragalus, 14, 391, 416 5 phalanx II; TMM 31263, at Sweeney Switch on road cut hwy 9, George West to Dinero Rd., Live Oak Co.: Nos. 2 L upper M, 7 R upper P; TMM 31039, Lapara Creek, Live Oak Co.: Nos. 1, 2 R upper and lower P; TMM 40539, S. F. Austin Park: No. 4 L lower P; TMM 31132, Site 17, Bridge Estate, Bee Co.: Nos. 70 L ramus with P_2-P_4, 306 L juvenile ramus with D_2-D_4, 82, 131, 189B, 245A, F, 223, 275, 468, 551, 609 5R and 6L upper M, 22B, 42, 49, 66, 82, 151, 189A, 223, 245E, 383, 402, 432, 469, 495, 569 6R and 9L upper P, 3, 245C, 327, 351 L and 3R upper P or M, 49, 132, 292 3R P^2, 492 RD^2, 118, 210, 245B L and 2R M^3, 117, 326, 379, 440 L and 3R upper D, 53, 64, 91, 287, 338, 354, 423, 467, 558, 593 5R and 6L lower M, 114, 130, 162, 211, 251, 335, 345, 380, 384, 441, 546, 579, 613 8L and 8R lower P, 64, 121 2R P_2, 386 L D_2, 276, 369 2L M_3 102, 194, 155, 591 2R and 3L lower D, 185, 566 MT III, no no. distal metapodial, 5, 75, 167, 314, 415, 446 5 astragali, 109, 257, 388 phalanx II; TMM 31170, Site 19, Bee Co.: Nos. 49 R juvenile ramus with D_2-D_4, 41 L P_2-M_3, 112 R P_2, 74 R M_3, 17, 91 2R lower P, 55, 72 4L lower M, 90D L P^2, 90B, 71C, 111D, 3L M^3, 16C, 54E, 71D, 90E R and 3L upper P, 71E R upper M, 4, 127 MT III, 103, 115 phalanx II; TMM 31184, Site 18, Bee Co.: Nos. 19 R lower D, 10 R upper P; TMM 31390, 0.5 mi SW of Normana on Medio Creek: No. 2 L lower P; TMM 31081, Site 15a, Farish Ranch, Bee Co.: Nos. 7 R juvenile ramus with D_2-M_2, 780 R ramus with P_2-M_3, 1089 L P_2-M_3, 214 R and L D^2-D^4, 456 L juvenile ramus with D_2-M_1, 1044 L ramus with P_2-P_4, 637 R ramus with P_2-M_3, 638 L juvenile ramus with D_2-M_1, 520 L P^3-M^3, 527 R ramus with P_2-M_3, 516 L ramus with P_2-M_3, 729 L lower P and 2L lower M (one series), 1223 R ramus with P_3-P_4, 1076 R P^2-M^3, L P^4-M^3 (possibly one individual), 560 L ramus with P_2-P_3, 151 L juvenile ramus with D_2-M_2, 154 L ramus with P_2-M_1, 217 R ramus with P_2-M_3, 619 R P^2-M^1, 858, 865 2R P^2, 272, 291, 329, 559, 785, 857B, 1115, 1116, 1159E, 1251, 1288, 1441, 1472B, 1500 6L and 8R upper M, 223, 272, 291, 376, 595, 827, 857A, 1114, 1251, 1390, 1465, 1472A, C 5L and 8R upper P, 390, 857 2R upper P or M, 620, 627, 1009 L and 2R M^3, 272, 951, 1120, 1359 L and 3R upper D, 1015, 1291 R and L D^2, 117, 625, 722, 1031, 1412 2R and 3L lower M, 168, 643, 1071, 1515 2L and 2R lower P, 1010, 1464 R and L M_3, 709, 1225 L and R lower D, 775, 1062, 1179, 1352 4 MT III, 1366 distal MT III, 305 proximal MT III, 61, 699, 760, 855, 877, 960, 1450, 1516, 1324 9 astragali, no no., 59, 192, 351, 762, 875, 1095, 1271, 1232, 1449 10 calcanei, 210, 239, 765, 812, 1032, 1087, 1319 7 phalanx II; TMM 30896, Site 1, Buckner Ranch, Bee Co.: Nos. 536 R D^2-D^4, 495 R juvenile ramus with D_2-D_4, 240 R juvenile ramus with D_2-D_4, 533, 420G 2R P_2, 344, 417B 2R M_3, 344, 417A L and 2R lower M, 344B, J, K R and 3L lower P, 340B, J, 393 L and 2R P^2, 392 L M^3, 446 R D^2, 340E, F, G, J, 395, 397 2R and 4L upper P, 354A, B, C, 396, 457, 537 7L upper M, 537 R upper P or M, 145 MT III, 348, 379 2 astragali, 373B calcaneum.

Diagnosis. (Leidy, 1856, 1869, Gidley, 1907, according to Osborn, 1918, revised and completed): Hypsodont. Protocone isolated, elliptical, anteroposterior diameter twice as great as transverse. Protoconule, metaconule and fossette borders complicated. Hypocone small, about half the size of the protocone. Molars compared to premolars small. Lower teeth with wide, flaring metaconid-metastylid column, low labial groove in the premolars, deep in the molars. Pli caballinid and parastylid well developed, additional plications in flexids common.

Description. The sample of *Neohipparion,* which together with *Nannippus* and *Pseudhipparion* is the most common horse in the LPC fauna, is referred to the widespread species *N. occidentale.*

The styles of the ectoloph are strong. In the premolars the occasionally posteriorly directed parastyle is grooved, and the mesostyle is slightly bifurcate in early wear. In the molars the parastyle is grooved, the mesostyle pointed. There is a slight to marked metastyle in the premolars.

The protocone of the premolars is long and narrow, often markedly concave lingually. In the molars the protocone may be oval-lenticular, rather like in *Nannippus.* In early wear the protocone often has a spur directed toward the protoconule, or the protocone is anterolabially oblique. It does not connect to the protoconule until close to the base of the tooth, or at a mesostylar height of ± 1.00.

The hypocone is well constricted from the metaloph by a labial groove and a deep hypoconal groove, which sometimes almost meet between the hypocone and metaconule. The hypostyle often sends numerous plis dihypostyle lingually, partly closing off the groove, but I have not observed a hypoconal lake. A hypoconal lake does occur in M^3 as in *Nannippus* cf. *N. ingenuum.* Only in much-worn teeth is the groove obliterated; it can be traced to 1.00 or less from the base.

The plication frequency is high (table 22), the pli caballin is often multifurcated in the premolars, simple or bifurcated in the molars. In the premolars there is a tendency for the prefossette to open lingually in the postprotoconal valley; this can also be seen in the type of the species (Osborn, 1918, fig. 140). There is occasionally an open, in late wear closed, hypostylar fossette.

The lower cheek teeth have flattened labial markings of the protoconid and hypoconid, anteroposteriorly long, narrow flexids, well developed pli hypoconid in the premolars, and pli caballinid. In *N. occidentale* the pli caballinid is longer than in *N.* cf. *N. ingenuum.* It is prominent in the premolars, incipient in the molars. In the premolars the metaconid-metastylid column is wide and flaring with rounded-oval metaconid and angularly-rounded metastylid. Webb (1969, p. 104) commented on the difference in morphology between lower teeth of *N.* cf. *coloradense* from Burge and *N. occidentale* from Minnechaduza, and noted the pendant metaconid in *N.* cf. *coloradense,* in contrast to the anteriorly directed metaconid in *N. occidentale.* In *N. occidentale* from LPC both types occur, and especially in early wear the metaconid and metastylid may both droop slightly.

The paralophid frequently has a posteriorly directed plication, and the premolars in early wear, and occasionally the molars also, may have a posterior plication on the metaconid-metastylid commissure. There is often a prominent pli hypoconid opposite the pli caballinid of the premolars, and plications occur lingually between the metaconid and metastylid, anterolabially from the metaconid between the metaconid and the commissure, and on the commissure protruding anteriorly into the metaflexid. Usually the labial borders of the flexids are crenulated.

The lingual wall of the entoconid is on a level with or labial of the metaconid and metastylid. This was a character pointed out by Webb in *N. occidentale* from Minnechaduza, but it is more noticeable in *N. occidentale* from LPC, and more similar to the arrangement in the teeth of *N. eurystyle.* The entoconid tip is long and often bifurcated in the little-worn premolars.

The labial groove between the protoconid and hypoconid is deep in the molars, almost meeting the wide lingual groove between the metastylid and metaconid; in the premolars the labial groove is shallow.

Milk teeth. The milk teeth are similar to those of *N.* cf. *N. ingenuum,* but are more plicated. In the uppers both the parastyle and mesostyle may be grooved and the posterior wall is sometimes complicated with multiple plis dihypostyle, isolated hypostylar fossette, and crenulated enamel. As in *Nannippus* the fossettes may remain open, and the protocone of D^2 is often connected throughout wear. The protoconal spur of D^3-D^4 is more marked in *Neohipparion* than in *Nannippus* and the protocone longer.

The lower milk teeth are also more plicated than those of *Nannippus.* The paralophid is straight and the flexids well developed, often with enamel crenulations; the entoconid tip may be furcated with several forks. A pli caballinid occurs, especially in D_2. The parastylid is very large, and there is always a well developed protostylid.

Limb bones. The referred metapodials are proportionally slender. In MT III one of eight specimens lacks a facet for the mesocuneiform. The proximal medial phalanx cannot be separated from those of *Nannippus* and *Pliohippus (Astrohippus) martini* of closely similar size, but are not as long and slender as those referred to *P.* cf. *P. supremus,* and lack the large, flattened V-scar of the latter. All limb bones are proportionally smaller than those of *N.* cf. *coloradense* and *N. occidentale* from Burge and Minnechaduza.

Discussion. Neohipparion occidentale from LPC is smaller than most forms of this species. The tooth crowns are approximately 5.00 high, and thus lower than the crowns in the Minnechaduza sample, but hypsodonty is only slightly less in the LPC sample. The enamel configuration of the teeth from LPC seems more advanced toward *N. eurystyle* than that in the teeth from Minnechaduza; this was also commented on by Webb (1969, p. 111). This is evident in the stronger development of the pli caballinid and other plications of the lower teeth, and of the metastyle in the uppers. In *N.* cf. *coloradense* from Beaver (Hesse, 1936), which Webb identified with *N. occidentale,* the pli caballinid is also weaker, and is, for instance, absent in the teeth of the jaw figured by Hesse (1936, fig. 7). However, in size of the teeth and form of the protocone the Beaver sample rather resembles *Nannippus* than *Neohipparion.*

TABLE 29.–STATISTICS OF THE LIMB BONES,
Cf. *MERYCHIPPUS GUNTERI*, B

Variate	N	M	σ	V	OR
Astragalus dist. br.	2	2.53			2.51, 2.54
Height	2	2.42			3.40, 3.43
Calcaneum tuber. br.	1	2.54			2.54
Phalanx 1 dors. length	5	3.36 ±.053	0.119	3.55	3.18- 3.45
Least br.	5	1.58 ±.042	0.096	6.08	1.46- 1.73
Phalanx 2 volar length	5	2.30 ±.078	0.175	7.61	2.12- 2.46
Br.	4	1;82			1.72- 1.94

TABLE 30.–STATISTICS OF THE LIMB BONES,
Cf. *MERYCHIPPUS VETUS*, B

Variate	N	M	σ	V	OR
Radius dist. br.	1	3.58			
MC III prox. br.	2	2.34			2.23, 2.45
Prox. a-p.	1	1.88			1.88
Tibia dist. br.	1	3.84			
MT III length	5	19.0			18.3 -19.8
Prox. br.	5	2.31 ±.048	0.108	4.69	2.10- 2.45
Prox. a-p.	4	2.05			1.90- 2.12
MT-MC dist. br.	10	2.08 ±.039	0.122	5.87	1.92- 2.27
Astragalus dist. br.	3	2.50			2.42- 2.63
Height	4	3.41			3.32- 3.47
Calcaneum height	3	7.16			6.84- 7.44
Tuber br.	6	2.56 ±.051	0.124	4.84	2.44- 2.75
Phalanx 1 dors. length	9	3.78 ±.041	0.122	3.22	3.62- 4.01
Least br.	9	1.60 ±.040	0.120	7.49	1.44- 1.79
Phalanx 2 volar length	10	2,53 ±.042	0.134	5.29	2.32- 2.80
Br.	9	1.83 ±.054	0.163	8.90	1.58- 2.08

Neohipparion occidentale from the Ogallala type locality (Hesse, 1935) is quite similar to *N. occidentale* from LPC in enamel pattern, but the metastyle of the uppers and the pli caballinid of the lowers are even more developed, and the teeth are larger. This form must be close to *N. eurystyle.*

Clarendon *N. occidentale* is even slightly larger than *N. occidentale* from Minnechaduza and more hypsodont, index 27.8. The plication count is not as high as in the teeth from Minnechaduza, and somewhat lower than the count in the LPC sample. The protocone is very long, narrow, and markedly concave. In the lower teeth a pli caballinid is as often developed as in the LPC sample. A number of metapodials form a scatter together with LPC specimens referred to *N. occidentale.* In all of the eight MT III the facet for the mesocuneiform is developed.

TABLE 31.–STATISTICS OF THE LIMB BONES,
Cf. *MERYCHIPPUS CIRCULUS*, CS

Variate	N	M	σ	V	OR
Radius length	2	22.4			20.7, 24.0
Prox. br.	2	4.12			3.95, 4.29
Dist. br.	2	4.00			3.89, 4.11
MC III prox. br.	2	2.41			2.30, 2.51
Prox. a-p.	2	1.79			1.72, 1.86
Astragalus dist. br.	5	2.66 ±.029	0.065	2.44	2.58- 2.73
Height	6	3.74 ±.104	0.255	6.80	3.50- 4.17
Calcaneum height	2	7.67			7.25, 8.08
Tuber br.	1	2.76			
MT III length	2	22.5			22.4, 22.5
Prox. br.	2	2.82			2.70, 2.94
Prox. a-p.	1	2.64			
MT-MC distal br.	3	2.36			2.31-2.41
Phalanx 1 dors. length	5	4.13 ±.079	0.178	4.31	3.89-4.35
Br.	5	1.68 ±.056	0.125	7.41	1.53-1.78
Phalanx 2 volar length	3	2.89			2.72-3.08
Br.	3	2.00			1.98-2.03

The Evolution of the Equidae on the Texas Gulf Coastal Plain

It is uncertain whether the Texas Gulf Coastal Plain in fact is the cradle of the advanced horses, i.e., the merychippines, hipparions, and equines, as Quinn (1952, 1955) and Wilson (1959) presumed. Wilson believed that the ancestry of *Merychippus* evolved in the southeast and that the genus was an immigrant in the Great Plains, where it occurs in the Early Hemingfordian. Wilson stressed the significance of the crochet, which in a certain percentage of the little-worn or unworn teeth of *Parahippus leonensis* already is connected to the protoloph and often is connected in much-worn specimens, and believed that this species is ancestral to *Merychippus,* of which a connected crochet throughout wear is diagnostic.

A crochet occurs first in Chadronian *Mesohippus* as a short anterior plication on the metaloph; this is the stage of development in most later anchitheriines, i.e., Brulean *Mesohippus, Miohippus, Anchitherium, Hypohippus, "Megahippus,"* and *Archaeohippus.* The occurrence of this plication varies in different populations, but its frequency is generally low; it may have had some significance as a surface-increasing feature. The spread of the crochet plication took place chiefly in the genus *Parahippus,* but also in some other lines of descent; the following stage in the evolution of the crochet in the crochet in the Equidae was the connection of the crochet to the protoloph. The connection was apparently first established low down on the protoloph and accordingly showed up only in the worn teeth; finally it reached the

TABLE 32.–STATISTICS OF THE LIMB BONES,
Cf. *MERYCHIPPUS* SP. NEAR *HIPPARION* CS

Variate	N	M	σ	V	OR
Astragalus dist. br.	5	2.27 ±.057	0.128	5.62	2.11- 2.42
Height	4	3.17			3.03- 3.28
Calcaneum height	1	6.56			
Tuber br.	2	2.46			2.43, 2.48
MT-MC distal br.	3	1.95			1.82- 2.06
Phalanx 1 dors. length	2	3.44			3.35, 3.52
Least br.	2	1.35			1.32, 1.37
Phalanx 2 volar length	14	2.26 ±.025	0.093	4.11	2.08- 2.40
Br.	14	1.60 ± .030	0.114	7.09	1.40-1.78

TABLE 33.–STATISTICS OF THE LIMB BONES,
Cf. *CALIPPUS FRANCISI*, B and CS

Variate	N	M	OR
Calcaneum height	1	6.24	
Tuber br.	3	2.25	2.19 -2.29
Phalanx 1 dors. length	2	3.76	3.70, 3.81
Least br.	2	1.22	1.20, 1.24

TABLE 34.–STATISTICS OF THE LIMB BONES,
Cf. *CALIPPUS REGULUS*, LPC

Variate	N	M		V	OR
MC III length	1	13.4			
Prox. br.	1	1.80			
Prox. a-p.	1	1.50			
Astragalus dist. br.	5	1.86 ±.025	0.055	2.94	1.77- 1.91
Height	5	2.64 ±.034	0.076	2.87	2.51- 2.70
Calcaneum height	1	5.26			
Tuber br.	2	1.83			1.79, 1.87
MT III length	1	13.9			
Prox. br.	3	1.77			1.62- 1.89
Prox. a-p.	3	1.49			1.32- 1.64
MT-MC distal br.	2	1.47			1.45, 1.49
Phalanx 2 volar length	2	1.71			1.69, 1.72
Br.	1	1.29			

top of the protoloph. *Archaeohippus blackbergi* differs from other Equidae in that the crochet is often present in the permanent uppers, but does not connect to the protoloph even in much-worn specimens, although in the milk teeth the crochet does connect in some specimens. Partly on the basis of the well developed crochet White (1942) assumed *A. blackbergi* to be ancestral to ThF *Parahippus*, and Quinn (1955) and Bader (1956) concurred. The teeth of *Archaeohippus* are specialized in some regards and primitive in others, for instance the reduction of M^3_3 relative to M^2_2 is characteristic of *A. blackbergi* (and probably of the genus as a whole) and not shared by *P. leonensis* or any other *Parahippus* known to me. The genus probably did not give rise to new groups, but was an evolutionary blind alley. The ancestry of *Parahippus* and thus of the advanced horses, should be sought in the genus *Miohippus* as Stirton (1940, p. 170) maintained.

In *Parahippus* we may be able to follow the segregation of the connected crochet; however, this process was not complete even in some early forms of *Merychippus*. The final, rapid increase in frequency of the connected crochet probably took place in the genus *Merychippus*, and may have been correlated with the spectacular increase in crown height in this genus. It probably evolved as a consequence of increased demands on stability of the hypsodont tooth crown. In some advanced horses, such as hipparions and pliohippines, the crochet is occasionally disconnected in early wear, especially in the premolars.

The frequency of the precociously connected crochet alone is not an infallible criterion for separating *Parahippus* and *Merychippus*, since the increase in frequency of this character was gradual and frequencies probably varied between contemporaneous forms. Other characters, such as increase in the presence of a crochet, segregation of the connected metaloph, and increase in crown height, also evolved gradually, and not all simultaneously. All characters of the teeth have to be weighted equally, but it seems likely that with a complete *Parahippus-Merychippus* fossil transition the boundary between the genera will be arbitrary.

Large samples of *Parahippus* from the Great Plains, similar to the samples of *P. leonensis* from GG and ThF, have not earlier been statistically studied for possible high frequencies of the connected crochet. In a large sample of *Parahippus* from the Hemingford Quarries, Nebraska, the frequency of the connected crochet is similar to that in *P. leonensis*, while in a sample of *Parahippus* from the Lower Hemingfordian Bridgeport Quarries, Nebraska, this frequency is very low. In comparison with these forms *P. leonensis* appears to be late and progressive, rather than precociously early in development of the connected crochet.

The taxonomic relationship between *Parahippus leonensis* and the equally advanced parahippines of the Plains, for instance *P. coloradense*, *P. avus* (which according to Downs, 1956, pp. 246-247, may be ancestral to *Merychippus brevidontus)*, and *P. crenidens*, all of which seem little different from *P. leonensis* in tooth height, amount of cement and complication of the enamel, is not known, nor the relationship between the early merychippines, such as *M. gunteri*, *M. primus*, *M. tehachapiensis*, etc. It is possible that advanced *Parahippus* in different parts of the range of the genus evolved

TABLE 35.–STATISTICS OF THE LIMB BONES,
Cf. *PLIOHIPPUS MARTINI*, LPC

Variate	N	M	σ	V	OR
MC III length	5	17.9 ±.25	0.559	3.12	17.1-18.4
Prox. br.	5	2.85 ±.056	0.126	4.40	2.68- 2.98
Prox. a-p.	5	2.20 ±.060	0.135	6.14	2.09- 2.44
Astragalus dist. br.	11	3.12 ±.029	0.096	3.08	2.92- 3.25
Height	10	4.19 ±.035	0.111	2.65	4.01- 4.37
Calcaneum height	9	7.73 ±.093	0.279	3.61	7.29- 8.12
Tuber br.	15	2.89 ±.033	0.129	4.45	2.58- 3.08
MT III length	6	20.9 ±.204	0.500	2.42	20.3- 21.7
Prox. br.	6	2.94 ±.054	0.133	4.52	2.76- 3.10
Prox. a-p.	4	2.58			2.39- 2.72
MT-MC distal br.	11	2.52 ±.028	0.092	3.65	2.37- 2.67
Phalanx 2 volar length	15	2.87 ±.039	0.152	5.30	2.69- 3.24
Br.	16	2.24 ±.027	0.106	4.73	2.03- 2.40

into the more hypsodont *Merychippus* (Simpson, 1932, p. 27, Stirton, 1940, pp. 179-180, Downs, 1956, p. 247), although the number of different species involved in the transition may not have been as large as it appears from the current taxonomy of the fossil horses.

Quinn (1955, p. 64) in contrast to Wilson believed that *Merychippus* evolved in the Great Plains from low-crowned horses of the genus *Hippodon*, which in Quinn's phylogeny includes advanced members of *Parahippus* and primitive *Merychippus* of orthodox nomenclature. This assumption does not, however, differ radically from Wilson's, since Quinn thought that the ancestral stock of Great Plains *Merychippus* was of Burkeville origin and probably descended from GG *"Hippodon vellicans"* (= *Parahippus leonensis* of this work). Quinn (1955, pp. 78, 80) placed *Merychippus* in his tribe Hipparionini, but believed that *Merychippus* as such did not occur in the Gulf Coastal Plain. He did not recognize *M. gunteri* of the B and CS faunas as a primitive merychippine, nor the occurrence of that genus in LPC. As questionably *Merychippus* he described (pp. 63-64) and figured (plate 1, figs. 13 and 1C) a lower tooth (TMM 40071-4) believed to have been found in the GG fauna. A renewed study of the specimen has shown it to be a deciduous D3 or D4 of either *Calippus* from CS or LPC or of *Pseudhipparion* from LPC, and probably misplaced in GG at labeling. The morphology is clearly that of a milk tooth: great length in comparison to breadth, well developed parastylid and slight protostylid, and traces of a labial cingulum. Characters of the metaconid-metastylid column (long, narrow metaconid, shorter, more rounded metastylid), somewhat flattened flexids, thick cement, slight pli caballinid, and considerable crown height are typical of *Pseudhipparion*. The protostylid is variable in that genus; in *Calippus*, which genus the tooth also resembles, a protostylid is said to be absent (Quinn, 1955).

Quinn (p. 80) further suggested that a milk dentition (TMM 31242-84) from B probably represents an early, *Merychippus insignis*-like hipparion, ancestral to *Hipparion* to which he referred (p. 57) two milk dentitions (TMM 31219-230 and -43) from CS. In all cases the specimens belong to advanced species of *Merychippus*. These species, *M. vetus* and *M. circulus*, he placed in three different genera *(Protohippus, Pliohippus,* and *Eoequus)* and assumed them to be taproots of separate phyletic lines. The morphological similarity between *M. vetus* and *M. circulus* indicates an ancestor-descendant relationship similar to the relationship between *M. seversus* and *M californicus* (Downs, 1961). *"Eoequus wilsoni" (= Merychippus circulus)* from CS is the species that Quinn (1955, p. 80) had in mind when stressing the importance of the Gulf Coastal Plain faunas as the source of the ancestry of *Equus*. However, Stirton (in letter to Wilson) believed that *"Eoequus"* "has nothing to do with the ancestry of *Equus*." Characters of the teeth suggest that *M. circulus* may have been the ancestor of *Pliohippus (Astrohippus) martini*.

Quinn (1955) referred the hypodigm of LPC *Pliohippus martini* to four or five species and three genera. Two genera, *"Equus"* and *"Hippotigris,"* he derived (fig. 3) more or less directly from *"Eoequus,"* and LPC *"Protohippus perditus"* he derived from *M. vetus*. The types of Quinn's species differ, as Webb (1969) pointed out, in the stage of wear of the teeth. *Pliohippus martini* is an advanced, in many features *Equus*-like pliohippine, but whether this line later evolved on into *Equus* is a remote question, which cannot be settled on the basis of the data at hand. McGrew (1944) discussed the ancestry of *Equus* s. l., and thought that *Equus* s. s. evolved from *Pliohippus (Astrohippus),* and *Hippotigris* from *Pliohippus (Pliohippus)* through *Plesippus*. He regarded the absence of a hypostylid in the lower D of *Equus* s. s and its presence in *Hippotigris* as a distinguishing character. In LPC *P. martini* the hypostylid is variable, but it is usually weak or absent, whereas in *P.* cf. *P. supremus* the hypostylid is developed.

Thus in Quinn's opinion, *Merychippus* does not occur in the Texas Gulf Coastal Plain faunas or occurs questionably in GG; the hipparions probably originated in B and were certainly represented in CS, and the equines were represented by an already advanced ancestral form in CS, and by *Equus* s. s. in LPC.

The earliest merychippines in the Texas Coastal Plain faunas are *M. gunteri* and the more advanced *M.* sp. and *M. vetus* in the B fauna. The merychippines were especially abundant and differentiated in CS, where they comprised some 75 percent of the equids. *Merychippus gunteri* probably evolved in the southeast from *Parahippus leonensis*, but *M. vetus* seems to have been an immigrant. The closer relatives of this species should be looked for among the merychippines in the Great Plains and on the Pacific Coast. *Merychippus* sp. near *Hipparion* is probably immigrant, although in some primitive features it resembles *M. gunteri*. Primitive, low-crowned *Merychippus* survived in CS and LPC; in the latter fauna a few isolated teeth evidence the genus.

The hipparions appeared for the first time on the Texas Coastal Plain in the LPC fauna and were already advanced. Their earlier evolution must have occurred elsewhere. *Neohipparion* and *Pseudhipparion* probably evolved in the Great Plains, *Nannippus* may have originated in the southeast, although

TABLE 36.–STATISTICS OF THE LIMB BONES,
Cf. *PLIOHIPPUS* cf. *P. SUPREMUS*, LPC

Variate	N	M	σ	V	OR
MC III length	2	21.2			+20.9, 21.4
Prox. br.	1	3.25			
Astragalus dist. br.	8	3.29 ±.051	0.144	4.37	3.11- 3.55
Height	8	4.45 ±.033	0.092	2.08	4.30- 4.58
Calcaneum height	4	9.07			8.71- 9.44
Tuber br.	7	3.34 ±.071	0.187	5.58	3.16- 3.65
MT III length	4	23.8			23.3, 24.7
Prox. br.	3	3.18			3.05- 3.39
Prox. a-p.	2	2.83			2.75, 2.90
MT-MC distal br.	7	2.76 ±.043	0.113	4.11	2.67- 2.93
Phalanx 2 volar length	1	3.47			
Br.	1	2.70			

the genus is also represented on the Pacific Coast. Sondaar (1968) stressed that *Nannippus* may be heterogeneous and comprise forms belonging in *Hipparion* rather than in *Nannippus* as defined by Matthew. On the other hand, *Nannippus* could well be referred to *Hipparion* as a subgenus, and may have evolved from early *Hipparion*.

The earliest pliohippines appear together with the hipparions in LPC. *Pliohippus (Astrohippus) martini* may have evolved from *Merychippus circulus*, but *P.* cf. *P. supremus* is an immigrant which resembles northern forms of the genus. *Equus* is not represented in the Gulf Coastal Plain faunas studied.

Although Quinn (1955, p. 76) believed that the LPC fauna "must have furnished the stock that replaced *Merychippus* in the north and west at that time" (i.e., the beginning of Pliocene time) there is no evidence to support his belief, and some evidence against it. The age of the LPC fauna in comparison to the faunas of the Great Plains is decisive. Although Quinn noticed close similarities in composition of the faunas of LPC and Burge, Nebraska, he considered the former older than the latter after comparing the hypsodonty of the horses. Quinn's conclusions as to the hypsodonty of the Burge and LPC horses are not confirmed by my data. On the contrary, according to my data all LPC horses, except *Merychippus* sp., are advanced in hypsodonty over the corresponding forms in the Burge. Although greater hypsodonty does not necessarily indicate younger relative age, since it may reflect ecologic differences in contemporaneous forms, the LPC horses are more advanced than their Burge equivalents in both hypsodonty and enamel pattern. *Neohipparion occidentale* is advanced in enamel pattern over *N.* cf. *coloradense* from Burge (Webb, 1969) and even over *N. occidentale* from Minnechaduza, although not fully as hypsodont. The LPC fauna could not have furnished the stock ancestral to the Pliocene horses, since more primi-

TABLE 37.–STATISTICS OF THE LIMB BONES,
Cf. *NANNIPPUS* cf. *N. INGENUUM*, LPC

Variate	N	M	σ	V	OR
MC III length	8	16.8 ± .141	0.400	2.39	16.2- 17.3
Prox. br.	8	2.50± .042	0.119	4.77	2.28- 2.63
Prox. a-p.	8	1.91± .041	0.116	6.05	1.72- 2.07
Astragalus dist. br.	1	2.51			
Height	1	3.31			
Calcaneum height	3	6.50			6.41- 6.55
Tuber br.	5	2.43± .019	0.042	1.72	2.41- 2.50
MT III length	4	18.1			17.9- 18.5
Prox. br.	4	2.47			2.40- 2.56
Prox. a-p.	4	2.16			2.05- 2.22
MT-MC distal br.	12	2.17± .047	0.163	7.51	1.86- 2.35

TABLE 38.–STATISTICS OF THE LIMB BONES,
Cf. *NEOHIPPARION OCCIDENTALE*, LPC

Variate	N	M	σ	V	OR
MC III length	1	±20.7			
Prox br.	1	2.54			
Astragalus dist. br.	14	2.68± .025	0.094	3.50	2.53- 3.03
Height	12	3.69± .036	0.125	3.39	3.48- 3.86
Calcaneum height	5	7.18± .049	0.109	1.52	7.05- 7.33
Tuber br.	8	2.61± .023	0.064	2.45	2.53- 2.68
MT III length	9	21.2 ± .246	0.737	3.48	20.0- 22.6
Prox. br.	10	2.60± .040	0.127	4.90	2.41- 2.75
Prox. a-p.	7	2.40± .051	0.135	5.63	2.32- 2.55
MT-MC distal br.	9	2.25± .024	0.071	3.16	2.12- 2.32
Phalanx 2 volar length	15	2.63± .039	0.150	5.70	2.38- 2.97
Br.	15	1.89± .022	0.087	4.60	1.70- 2.01

tive ancestral forms occur in the Great Plains.

Of Great Plains Clarendonian forms absent in the Texas Gulf Coastal Plain *"Megahippus"* is a noticeable example. This large anchitheriine is also absent in the Clarendon fauna of North Texas. As a whole the large anchitheriines, *Anchitherium* and *Hypohippus*, are rare in the Texas Coastal Plain, Florida, and North Texas faunas if compared with the bulk of fossil horse material collected; while seldom common in the northern faunas, they do appear more frequently in the material from the Great Plains. The faunas of the south may have been marginal habitats of these large browsers throughout the Miocene and Lower Pliocene.

TABLE 39.–REVISED LIST OF THE EQUIDAE OF THE TEXAS GULF COASTAL PLAIN

Garvin Gully	**Thomas Farm**
Archaeohippus blackbergi	*Archaeohippus blackbergi*
Anchitherium navasotae	*Anchitherium navasotae*
Parahippus leonensis	*Parahippus leonensis*
Parahippus cf. *P. texanus*	
Burkeville	
Anchitherium navasotae	
Cf. *Parahippus* cf. *P. texanus*	
Merychippus gunteri	
M. vetus	
M. sp. near *Hipparion*	
Calippus francisi	
Cold Spring	
Merychippus gunteri	
M. circulus	
M. sp. near *Hipparion*	
Calippus francisi	
Lapara Creek	**Clarendon (Webb, 1969, Table 1)**
Hyohippus affinis	*Hyohippus affinis*
Merychippus sp.	*Calippus regulus*
Calippus regulus	*Pseudhipparion aff. gratum*
Pseudhipparion sp.	*Astrohippus martini*
Pliohippus (Astrohippus) martini	*Pliohippus supremus*
P. (Pliohippus) cf. *P. supremus*	*Dinohippus fossulatus*
Nannippus cf. *N. ingenuum*	*Hipparion* cf. *plicatile*
Neohipparion occidentale	*Neohipparion occidentale*

Characteristics and Correlation of the Coastal Plain Faunas

Patton (1969) recently revised the relative age of the Texas Gulf Coastal Plain faunas on evidence part of which was not known to Quinn (1955). Patton arrived at a younger age for each local fauna than Quinn did. The present study has revealed little to change his general conclusions; some minor changes may be discussed.

The horses in the GG fauna are brachyodont. *Anchitherium navasotae* corresponds in size to Arikareean *A. agatense* from Agate Springs, Neb., and to Hemingfordian *A.* cf. *agatense* from Flint Hill, S. D.; however, in this group of horses there was little change in size throughout the Lower and Lower Middle Miocene. *Archaeohippus blackbergi* is one of the smallest species of its genus, and geographically rather isolated. Harksen and McDonald (1967) referred *A.* cf. *blackbergi* from Flint Hill, and Downs (1956, p. 255) compared *A. penultimus* from Sheep Creek, Neb., to *A. blackbergi* and observed a close similarity, although *A. penultimus* is larger. There may have been a slight gradual increase through time in size of the teeth of this genus (Downs, 1956); *A. blackbergi* is among the smallest forms known, which could be a primitive character. *Parahippus leonensis* is an advanced species of its genus and as progressive as Middley Miocene forms from the Great Plains.

It is now evident that *Merychippus* is not a member of the GG fauna, as its occurrence there (Quinn, 1955, pp. 63-64) was based on a misidentification. Nor is this genus found in the related ThF fauna, although *M. gunteri* was reported from ThF by White (1942), Quinn (1952), Downs (1956), and Patton (1969). Bader (1956), after a careful statistical study, concluded that there is no reason to split the *P. leonensis* sample from ThF (see also Simpson, 1932, p. 23). Quinn (1952) used the assumed occurrence of *M. gunteri* in ThF as evidence for assigning a slightly younger age to ThF than to the GG. According to Patton (1967, p. 184) the ThF fossil assemblage is heterochronic with a fauna of the deeper portions of the dig corresponding to GG, and a slightly younger, upper fauna more resembling B. Bader (1956) mentioned that the small tooth specimens of *P. leonensis* generally came from the deeper layers, with increased size characterizing the teeth from the upper beds. There is no apparent correlation, however, between the size of P^3_3-M^2_2 and such morphological characters as height of crown and connection of the crochet in the ThF sample of *Parahippus* teeth. Mean length of the teeth with a connected crochet is 1.51 ± .014, or insignificantly smaller than 1.53 ± .005 for the total sample. The GG sample mean 1.42 ± .008 is significantly smaller than 1.53 ± .005, but the frequency of the connected crochet is greater in P^3-M^2 from GG. Thus *P. leonensis* from ThF is no more advanced toward *Merychippus* in the connection of the crochet than is *P. leonensis* from GG, but the GG population may correspond more closely in size and proportions of the teeth and limb bones to the slightly earlier, smaller "form" at ThF. Patton seems to have based his opinion about the Hemingfordian age of GG and ThF mainly on the assumed occurrence of *Merychippus* in these faunas, but the evidence is inconclusive on the grounds mentioned above.

Simpson (1932, pp. 13-16) considered ThF to be Late Lower Miocene, and Wilson (1957, 1959, 1960) also placed GG in the Arikareean on the basis of the occurrence there of *Daphaenodon, Dinohyus,* and *Parahippus.* On the other hand, the occurrence of *Archaeohippus* would suggest a younger age, since other members of that genus are Middle or Late Miocene. On the basis of *Archaeohippus* Hesse (1942, p. 177) placed GG in the Hemingfordian. The assemblage of the three equids, *Anchitherium, Parahippus,* and *Archaeohippus,* is similar to that in the Lower Hemingfordian Bridgeport fauna, and in the fauna of Flint Hill (Harksen and McDonald, 1967). I have not seen the material of *P. cognatus* from Flint Hill, but *P.* sp. from Bridgeport is definitely more primitive than *P. leonensis.* On the basis of the horses, i.e., the absence of primitive *Merychippus,* but presence of advanced *Parahippus* and of *Archaeohippus,* GG and ThF seem to be Early Hemingfordian.

The B horses are subhypsodont or hypsodont and noticeably advanced over the GG forms, although *Merychippus gunteri* is similar to *Parahippus leonensis* in many features, as Simpson (1932, pp. 23-26) noted, and probably is the direct descendant of that species. *Merychippus gunteri* from the Texas Gulf Coastal Plain appears to be slightly more advanced, i.e., more hypsodont, than *M. gunteri* from the type locality Midway, Fla., but comparative material of the Florida form is scarce. Simpson (1932, pp. 26-27) compared *M. gunteri* with *M. primus* of the Middle Miocene Sheep Creek; on the other hand, *M. vetus* of B compares rather closely with Late Miocene Mascall *M. seversus* and approaches *M. californicus* of North Coalinga. *Calippus francisi* is a progressive equid with tall, slender crowns; this species is said to be common in the Niobrara River fauna (Webb, 1969). *Merychippus vetus* and *C. francisi* are immigrants in the Texas Coastal Plain, and so probably is *M.* sp., although it has characters in common with *M. gunteri.*

The age of B is rather uncertain as the material referred to this faunal zone appears to include faunas of somewhat different age. Faunas with only *M. gunteri* may be older than those with *M. gunteri, M. vetus, M.* sp., and *Calippus francisi.* This would explain the similarity of the "older" B faunas, i.e., those from Point Blank, Burkeville, and Barringer Farm, to the GG and ThF faunas, over which they appear to be only slightly advanced, and of the "younger" B faunas, i.e., from localities 4, 5, 6, and Summer's Pit, to CS with which they share species in common. Quinn (1955, p. 15, table 2, footnote) referred Summer's Pit to the "lower part of the Cold Spring faunal zone," but locality 4 (type locality of *"Protohippus" vetus* Quinn) he referred to B. According to Quinn (p. 15) locality 5 is "lower part of the Burkeville;" Patton (1969, p. 120, table 1, footnote 2), however, thought, on the basis of the fossils, that it "falls within the Cold Spring rather than Burkeville fauna."

"Older" B is distinguished by the presence of *Merychippus gunteri, Prosynthetoceras texanus,* and *Floridatragulus texanus,* all of which are advanced over, but closely related to, respective ancestral forms in GG and ThF (Patton, 1969). In the "younger" B occur *Calippus francisi, M.* sp., and *M. vetus,* the former two of which also occur in CS and the latter of which has a direct descendant, *M. circulus,* in CS. Unfortunately the B. collection is scant, as also Patton (1969) lamented on, and it is thus possible that only accidentally no advanced horses were collected at the Point Blank and Barringer Farm sites, and no specimens of *Prosynthetoceras texanus* and *Floridatragulus texanus* at localities 4, 5, and 6.

"Older" B seems younger than Midway because of the absence of *Archaeohippus blackbergi* and *Anchitherium navasotae,* both of which still occur at Midway, and the probably slightly lower crowns of the teeth of *M. gunteri* in the Midway sample. However, the absence of the anchitheriines may be only apparent and due to sampling error, since *Anchitherium navasotae* or a similar anchitheriine occurs in the Push Creek fauna together with *M.* sp. and *M. vetus.* Wilson (in letter), on the other hand, thinks *Anchitherium* may be reworked in the Push Creek.

Patton (1969) placed B in the Middle Hemingfordian. Patton's B (Point Blank) is equivalent to "older" B and is only little advanced over GG; it should be close also in time to that fauna. If "older" B is Middle Hemingfordian then GG should be Lower Hemingfordian as Patton maintained.

There has been some debate on the early occurrence of the genus *Merychippus* (see review in Patton, 1969, pp. 208-210). Sheep Creek *M. primus* is certainly a primitive representative, and not far removed from advanced *Parahippus.* The connected crochet is considered diagnostic of *Merychippus,* but in a sample of *M. primus,* in the University of Nebraska State Museum, the crochet is connected only in some 50 percent of P^3-M^2 and in 33 percent of M^3. In *M. gunteri* it is connected in all P^3-M^3 studied. In P^2 the frequency is low in both *M. primus* and *M. gunteri.* Although the frequency of the connected crochet probably varied in and between contemporaneous forms, *M. gunteri* does not seem to be earlier and more primitive than *M. primus,* especially since the latter is slightly less hypsodont (index 13.9).

"Younger" B is well separated from "older" B in regard to the horses, and is probably Lower Barstovian. The Push Creek and Balt Creek faunas with a mastodont, *Merychippus* sp. and *M. vetus,* large *Parahippus,* and *Anchitherium navasotae* may thus well be "younger" B, although mastodonts are absent in other local faunas of B and are generally considered indicative of a Barstovian age (Gazin and Collins, 1950). Renewed investigation of the "younger" B faunas may show them to be referable to CS rather than to B. The affinities of the horses are certainly with CS, and Patton (1969, p. 186) identified *Prosynthetoceras francisi,* a typical CS artiodactyl, from locality 5 of "younger" B.

Patton (1969) correlated the CS fauna with the Barstovian, a conclusion I completely agree with. The closer correlation in the Barstovian is more difficult; according to Patton (p. 213) CS probably represents the early to middle part of the Barstovian, and on p. 220 he placed it in "the interval between the Lower Snake Creek of Nebraska and the Pawnee Buttes of northeastern Colorado, the late Miocene portion of the Barstow "fauna" from California, and the Calvert fauna of Maryland." Quinn (1955, p. 75), on the other hand, placed CS in the Late Middle Miocene.

Merychippus circulus is as hypsodont as *M. californicus* or even slightly more advanced in crown height, but is probably closely related to *M. vetus* of the "younger" B, and a direct descendant of that species. *Calippus francisi* is common, and so is *M.* sp. with features of *Hipparion.* Some low-crowned teeth found throughout CS may represent *M. gunteri* or an equally primitive form.

The CS horses are not much different from those of the "younger" B; *Calippus francisi* and *Merychippus* sp. are identical in the two faunas, and *M. circulus* represents evolution in place.

The LPC fauna is separated from CS by a hiatus (Wilson, MS, Quinn, 1955, Patton, 1969). The horses are markedly advanced and have a definite

Pliocene character. The LPC marks the first occurrence in the Texas Gulf Coastal Plain of the hipparions *(Pseudhipparion, Nannippus,* and *Neohipparion)* and of pliohippines *(Pliohippus (Astrohippus)* and *P. (Pliohippus)). Merychippus* lingers on in brachyodont form, and *Hypohippus* occurs.

The LPC horses are more primitive than those described by Savage (1941) from the Optima fauna, Okla., and by Matthew and Stirton (1930) from Hemphill County, Tex. Some teeth of *Nannippus* cf. *N. ingenuum* are similar to those of *N. lenticulare,* but the sample as a whole is more primitive, for instance in crown height. *Pliohippus (Astrohippus) martini* and *Neohipparion occidentale* differ from the corresponding forms in the younger faunas; Hemphillian *N. eurystyle* is more extreme in development of the elongate, concave protocone and long pli caballinid, and *P. ansae* differs from *P. martini* in the simplified pattern and short protocone of the teeth, and in monodactyly. In the Great Plains Minnechaduza fauna *P. martini* apparently is monodactyl, although it is tridactyl in the LPC and Clarendon faunas. *Pliohippus* cf. *P. supremus* is not as hypsodont as *P. interpolatus,* but is approaching that species in tooth structure. *Pliohippus interpolatus,* however, is monodactyl in contrast to *P.* cf. *P. supremus.*

The LPC horses are similar to those described by Hesse (1936) from Beaver, Okla. Hesse's *Nannippus* sp. material (p. 64) is identical to *Pseudhipparion* in LPC (see, however, Webb, 1969, pp. 129-130) and the upper tooth of *Calippus* sp. (Hesse, 1936, p. 8) falls inside the size range of *C. regulus. Pliohippus (Astrohippus) martini* occurs in both faunas, but *Neohipparion occidentale* is more advanced than *N.* cf. *coloradense* from Beaver, which may correspond to *Nannippus* cf. *N. ingenuum* rather than to *Neohipparion.*

There is close correspondence between the horses from LPC and the Clarendon type-localities of Donley County, Tex. (table 39). In almost all cases the teeth of the Clarendon forms are slightly larger and slightly more hypsodont than in LPC, but the limbs are similar in size, proportions, and adaptation. The same species are probably represented, except that *Merychippus* does not occur in the Clarendon sample.

The LPC fauna may be slightly younger than Patton assumed it to be. Both Patton and Webb (1969) correlated LPC with the Lower Clarendonian Burge fauna, but the horses are more advanced than those Webb described from Burge. The hypsodonty index in the LPC sample of *Neohipparion occidentale* is closer to *N. occidentale* of Minnechaduza and Clarendon than to *N.* cf. *coloradense* from Burge, and *Pliohippus* cf. *P. supremus* has a higher hypsodonty index than *P. supremus* from Burge and Minnechaduza. The enamel pattern of the teeth of these LPC forms also is more advanced than in the corresponding samples from both Burge and Minnechaduza, and approaches Hemphill species of these genera. On the other hand, *P. martini* in the Minnechaduza is monodactyl and thus advanced over the LPC and Clarendon forms. The pooled evidence would place LPC closer to the Clarendon and Minnechaduza Late Clarendonian faunas than to the Burge Early Clarendonian fauna, and taxonomically especially close to the Clarendon fauna of North Texas.

SUMMARY AND CONCLUSIONS

Sixteen species of fossil horses belonging in four genera of the subfamily Anchitheriinae and five genera of the subfamily Equinae are described from the Garvin Gully, Burkeville, and Cold Spring Miocene faunas, and the Lapara Creek Pliocene fauna of the Texas Gulf Coastal Plain. The origin of the horses in the early, Garvin Gully, fauna is not known, but the genera represented, *Anchitherium, Archaeohippus,* and *Parahippus,* are widely distributed in North America. *Merychippus gunteri* in the Burkeville has been shown probably to have evolved from *Parahippus leonensis* (Simpson, 1932), and thus is an autochton. *Calippus francisi* and *M. vetus* do not have suitable ancestral forms in the Gulf Coastal Plain faunas known; both appear to have been immigrants. Possibly immigrant, but of uncertain origin, is *M.* sp. near *Hipparion;* this form could be ancestral to *Hipparion, Pseudhipparion* and *Nannippus,* the latter of which seems to have had its main distribution in the southeast, south, southwest, and west. *Hypohippus affinis, Pliohippus (Astrohippus) martini, P. (Pliohippus)* cf. *P. supremus,* and *Neohipparion occidentale* occur widely in the Clarendonian, and *Calippus regulus* is also found in North Texas. *Calippus regulus* may have evolved from local *C. francisi* through diminishing of size and increase in tooth height, and may thus represent evolution in place, but it may also be a small southern form of the widespread *C. placidus* (Webb, 1969). *Merychippus circulus* probably evolved locally from *M. vetus,* and this line could have continued on in *Pliohippus (Astrohippus) martini.* The Great Plains form of *P. martini* was monodactyl, although *P. martini* was tridactyl in the south.

Patton (1969) in his study of the Coastal Plain artiodactyls came to similar results, i.e., he observed frequent interchange between the Coastal Plain faunas and those of the Great Plains, but also some local differentiation.

The fossil horses of the Coastal Plain resemble both taxonomically and to their assemblage those from other parts of North America, especially assemblages from the Great Plains. The horses confirm Patton's (1969) correlation of the Coastal Plain faunas with faunas in other areas of North America, and give added weight to his conclusions, which were based on the fossil artiodactyls. The association of the three equid genera *Anchitherium, Archaeohippus,* and *Parahippus* distinguishes the Early to Middle Hemingfordian, and the appearance of primitive *Merychippus* indicates Sheep Creek age; a great variety of merychippine horses distinguishes the Barstovian, and the hipparions and pliohippines the Clarendonian faunas of the Texas Gulf Coastal Plain as well as in the Great Plains. Taxonomically there are similarities in that *Archaeohippus blackbergi* has also been referred from the Flint Hill fauna of the Middle Hemingfordian of South Dakota (Harksen and McDonald, 1967), *Calippus francisi* is common in the Niobrara River fauna (Webb, 1969), and the horses from the Lapara Creek are specifically identical to those from the Minnechaduza and Burge. Forms in common with the faunas of the southeast are *Anchitherium navasotae, Archaeohippus blackbergi,* and *Parahippus leonensis* in the Thomas Farm, and *Merychippus gunteri* in the Midway fauna of Florida; *Nannippus ingenuum* was originally described from the Alachua clays of Florida.

The Texas Gulf Coastal Plain may well have been a separate faunal province as maintained (Wilson, MS, Patton, 1969), but the interchange of faunal elements was extensive, especially in the Clarendonian. A long hiatus between the Cold Spring and Lapara Creek has been supposed on the basis of the faunal differences (Wilson, MS, Quinn, 1955, Patton, 1969), but whether the differences reflect the length of time between the Cold Spring and Lapara Creek not covered by fossil finds, or the sudden removal of possible earlier barriers (climatic as Wilson, MS, suggests) with subsequent influx of immigrant forms, is not known.

The evolution of the Equidae on the Coastal Plain as set forth by Quinn (1955) does not seem plausible, as there is little evidence that the Coastal Plain faunas were the sources of the ancestry of the advanced horses of the subfamily Equinae. *Archaeohippus blackbergi* is removed from the direct ancestry of the advanced horses because of its reduced M^3_3. The genus *Hippodon* in Quinn's phylogeny comprises forms of *Parahippus* and *Merychippus*. *Parahippus leonensis* is an advanced member of its genus, but there is equally advanced *Parahippus* in the Hemingfordian of the Great Plains; there is no clear evidence for the presumption that *P. leonensis* is ancestral to *Merychippus* s. l., although probably ancestral to *M. gunteri* (Simpson, 1932). The ancestry of *Merychippus*, and thus of the advanced horses, is to be sought in the genus *Parahippus;* the origin of *Merychippus* may have been polyphyletic in that different species of *Parahippus* may have reached an essentially merychippine stage of evolution. The evolution of the crochet, which has been considered decisive, began with the appearance and subsequent spread, probably through segregation of this character in certain lines of descent, of the crochet plication. The spread of the connected crochet took place in *Parahippus* and especially in *Merychippus*, but was not fully complete even in advanced horses, such as hipparions and pliohippines. Thus the connected crochet is not an infallible criterion for separating *Parahippus* and *Merychippus*, and all characters of the teeth, for instance hypsodonty, amout of cement, connection of the metaloph and ectoloph, and plication frequency, have to be weighted equally.

Merychippus was the dominant equid in the Late Miocene Burkeville and Cold Spring faunas, and occurs as a holdover in the Pliocene of the Lapara Creek. The latter fauna is characterized by advanced equines, the hipparions and pliohippines. These grazing horses seem to have evolved through a major radiation at the end of the Miocene and subsequently to have spread rapidly over the northern parts of the New and Old World continents.

Throughout the Miocene and Early Pliocene the large anchitheriines, *Anchitherium*, *Hypohippus*, and *"Megahippus,"* were rare in the Coastal Plain, and this area may have been a marginal habitat of these browsers.

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